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Seedling resistance of corn to leaf feeding of the European corn borer, Ostrinia nubilalis

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SEEDLING RESISTANCE OF CORN TO LEAF FEEDING OF

THE EUROPEAN CORN BORER, *OSTRINIA NUBILALIS*

by

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INTRODUCTION

The European corn borer, Ostrinia nubilalis (Hubner), is one of the most important insects associated with corn production throughout the corn belt. The extent of damage to the corn crop is estimated in the millions of dollars each year.

Much work has been accomplished on the corn borer problem since 1917 when this insect was first recognized in the United States. The first studies were conducted by entomologists who were concerned with the biology of the insect. However, it was soon realized that there was a need for studies on the agronomic aspects of the problem. Since that time, cooperative corn borer research has continued between these and other related fields. The studies presented in this paper are of a cooperative nature, between Agronomy, Entomology, and Botany.

Most studies of corn borer resistance have been conducted on corn plants in older stages of development, especially the mid-whorl and late whorl stages. The reason that older plants were used in these studies is probably the results of some of the earlier studies which showed low, insignificant rates of larval survival on plants infested in the earlier stages. However, most of these earlier studies were based on survival levels at or near the end of the larval development period and did not test plant resistance to early larval establishment on younger plants. A relationship between stage of plant growth and survival of corn borer larvae was suggested from these studies. Several workers reported that larvae were not able to survive on corn plants until they reached a height of about 16 inches. This seemed to indicate that survival was related to the time when the plant tassel was initiated.

Levels of plant resistance to early feeding by European corn borer larvae have been demonstrated among corn lines and strains in the more mature stages of plant growth. However, very little has been written concerning the effects of such resistance among plants in earlier stages of plant growth, particularly the seedling stage up to the time of tassel initiation.

These studies were conducted to determine (1) if there was any relationship between plant resistance to corn borer larvae and tassel initiation, (2) if relative levels of plant resistance among younger plants were similar to the levels demonstrated by older plants, (3) if resistance levels could be determined in the laboratory with the temperature and humidity controlled, using young plant tissues as the food source, and (4) if arrangements of certain leaf structures were correlated with corn borer resistance.

REVIEW OF LITERATURE

In order to understand an insect problem, one needs to know something about the life history and biology of the insect. Vinal (1917) was the first to report the presence of the European corn borer in the United States. At that time he described briefly some of the life stages, indicated the importance of this insect on corn, described the character of injury, presented a short sketch of the life history, and recommended some cultural practices as control measures. Vinal and Caffrey (1919) discussed these same topics in much more detail and presented other information on the biology of this insect. Vinal and Caffrey also recognized some natural enemies of the corn borer and reported on the use of certain chemicals as controlling agents.

Insect Biology

Early workers on the corn borer problem were interested primarily in the biology of the insect and the plant-insect relationships. Neiswander and Polivka (1930) reported that plant resistance is of two types; (1) resistance to oviposition and (2) resistance to survival. Huber et al. (1928), Patch (1929), Beard (1943), Beck and Lilly (1949), Turner and Beard (1950), Dicke (1950), Turner (1951), and Beck (1956c) reported that the stage of plant growth was important in determining amount of oviposition.

Plant resistance to larval survival has been studied in much detail by many workers. Caesar (1925), Huber and Savage (1931), Huber (1936), Tauber and Bruce (1946), and Dicke (1950) reported that the greatest mortality of larvae occurred just after the eggs hatched and before larvae were established on the plant. Beard and Turner (1942) described that period before establishment as a period when the larvae wandered about the plant looking for suitable places in which to become established.

Huber and Savage (1931) reported that the high mortality rate of young larvae probably was due to the morphological or chemical condition of their food or to high temperature and deficient moisture conditions, which cause excessive loss of body moisture, or a combination of both. Tauber and Bruce (1946) also recognized the period before establishment as a critical stage in the life cycle. They reported that, "During this pre-establishment period they [young larvae] are subject to whatever environmental and biological hazards may be present." These workers studied the environmental conditions of temperature and humidity as they are related to survival of young, unfed larvae. They concluded that temperatures between 70° and 90° F. with a relative humidity of 80 percent, or above, seem to be ideal for larval establishment in corn plants. Higher temperatures tended to increase larval activity and decrease longevity, and higher humidities tended to increase longevity directly. In their experiments, Tauber and Bruce found that unfed larvae were not able to survive longer than 71 hours when placed in a controlled environment where the temperature and relative humidity were maintained at 70° F. and 80 percent. Burditt and Holdaway (1959) reported that newly hatched larvae could not survive longer than 72 hours without food when kept at a temperature of 20° C. and a relative humidity of 80 percent.

The stage of plant growth at the time of infestation is important in determining the rate of larval survival as reported by Houser and Huber (1929), Neiswander and Polivka (1930), Polivka and Huber (1931), Schlosberg and Baker (1939), Beard and Turner (1942), Beard (1943), Patch (1947), Dicke (1950), and Luckmann and Decker (1952). It was generally concluded by these workers that survival of larvae was greatest on the older or earlier planted corn. In fact, Beard and Turner (1942), Beard (1943), Batchelder (1949), and Luckmann and Decker (1952) concluded that infestations of young plants before the mid-whorl or late whorl stages resulted in low survivals which were not significant. Beck (1960a) reported that plant "...resistance tends to decline and at about the time that the borers are well established in the tassel, the plant resistance is at a minimum."

Neiswander et al. (1928) reported that the stage of plant growth was important in determining where larvae become established on the plant. These workers reported that newly hatched larvae respond to at least two tropisms, a negative phototropic response and a positive trigmotropic response. These tropisms cause the larvae to move away from light and into areas of the plant where young leaf tissues are in contact with each other. The usual entrance into the young plants is by way of the whorl region. Neiswander et al. (1928), Beard and Turner (1942), Patch (1943), Batchelder (1949), Dicke (1954), Dicke and Guthrie (1955), and Beck (1956a) have reported that about 80 to 100 percent of the young larvae of the first generation which survived on plants before the late whorl stage could be found in the moist area of the whorl region. Beard and Turner (1942) reported that the tassels and developing ears offer good conditions for survival of young larvae on older plants.

Beck (1956b) summarized the plant-insect relationship by indicating that the plant and the insect are each separate biological systems which are changing constantly with regard to chemical and morphological composition and needs. Neiswander et al. (1928) reported that the food for the first and second instar larvae consists mostly of the young leaf tissues and second and third instars feed on the pollen buds. However, Dicke (1954) reported that the sheath is the primary feeding area of the third and fourth instar larvae and that little attack is made on the tassel until larvae reach the fourth instar. He further reported that little stalk invasion was evident until the larvae reached the fifth instar.

Neiswander and Huber (1931) reported that larvae compete with each other for food or shelter, or both. They showed an inverse relationship between the number of eggs applied and survival of larvae. Patch (1947) indicated that by adding three egg masses per plant higher rates of survival might be obtained, if plants were in a favorable stage for establishment, than by adding more than three egg masses per plant, if plants were in an unfavorable stage.

Laboratory Studies

Laboratory studies have been conducted on the European corn borer problem by many workers. Briand (1929) described a method of rearing larvae in the laboratory using tissues from various plants. Patch and Peirce (1933) described a method of producing corn borer egg masses in the laboratory for use in artificial infestation of plants in the field.

Huber (1938) in laboratory studies fed larvae etiolated leaf tissues from resistant and susceptible sources. He reported that larvae which were fed tissues from a resistant source, weighed less than half as much as larvae fed tissues from a susceptible source after nearly three weeks.

Bottger (1940 and 1942) studied the nutritional requirements of corn borer larvae and reported the development of a synthetic diet for use in laboratory studies. Beck (1947, 1953, 1956a, 1956b, 1956c, 1956d, 1960a, and 1960b), Beck and Stauffer (1950), Beck et al. (1949), Bect et al. (1957), Bottger (1951), and George (1957 and 1958) reported further studies on the nutritional requirements of corn borer larvae.

Beck and Lilly (1949) studied larval growth in terms of weight after 144 hours of feeding on cut sections of corn leaves which were rolled, placed in small vials, and kept at a temperature of about 85° F. They concluded that small resistant hybrids were less suitable as food for corn borer larvae than small susceptible hybrids, but these differences tended to disappear when plants are about 18 inches high.

Bottger (1951) fed larvae for 30 days on leaf tissues, internodes, and kernels from the same sources and recorded survival and average weights of larvae on several dates throughout the period. His data indicated that kernels consistently gave the best weights, and that leaves gave better weights than internodal tissues up to about 18 days. However, after this period internodes gave better weights than leaf tissues. Survival was slightly better on leaf tissues than on kernels, and both leaf tissues and kernels gave better survivals than internodes. These results showed a definite shift in the nutritional requirements of larvae as they matured.

Burditt and Holdaway (1959) described a laboratory method for evaluating corn borer resistance, using leaf tissues from plants in the mid- and late whorl stages. Round discs were punched from leaf tissues, pinned together, and placed in vials with known numbers of corn borer eggs which were ready to hatch. After hatching the larvae were kept at a temperature of 20° C. and relative humidity of 80 percent for 96 hours, at which time survival was determined. These workers also studied the effects of competition or crowding. They concluded that survival percentages were not significantly different between samples infested with 24.0 ± 3.4 eggs and samples infested with 40.9 ± 4.1 eggs.

Plant Damage

Turner and Beard (1950) summarized that corn borers damage plants in four major ways: (1) by destroying kernels; (2) by weakening stalks, ear shanks, and tassels so that wind breakage may occur; (3) by creating avenues for entrance of diseases; and (4) by causing physiological interference with plant growth. Holdaway (1956) reported that the first-brood of corn borer larvae generally reduced yield more than the second-brood, and that the second-brood was the best measure of population potential for the coming year. However, it was reported by Dicke (1954) that stalk breakage and ear droppage of present-day hybrids are mostly due to the second-brood corn borer larvae.

The association of micro-organisms in corn borer cavities was studied by Christensen and Schneider (1950). They observed many micro-organisms in the frass where corn borer larvae had been feeding and found a high correlation between stalk rot organisms and corn borer infestations. Dicke (1954) reported that those inbreds or hybrids which stand well under attack of stalk rot, also have good standability under attack of second-brood corn borer infestations.

Chiang and Holdaway (1959) showed that corn borer infestations reduced the size of corn leaves and length of internodes, and that tasseling and silking dates were delayed on resistant and susceptible single cross plants. These reductions in leaf size and internode length were observed while the larvae were still feeding on the leaves and before they had entered the stalk. This fact indicated that normal growth processes of the whole plant are influenced by feeding of young corn borer larvae on leaf tissues.

Chaing and Hodson (1953) described three types of leaf feeding by young larvae. There are: (1) pin hole feeding where punctures are very small and do not extend completely through the leaf tissues; (2) shot hole feeding where punctures are somewhat larger, extend through the leaf, and appear nearly round; and (3) large feeding holes where the lesions are rather long, narrow, and parallel to the leaf veins. Dicke (1954) reported that types of feeding lesions were different on resistant and susceptible plants. He reported that lesions on resistant plants tend to be small and round or narrow and elongate, and lesions on susceptible plants tend to be larger and elongated.

Methods of Rating Corn Borer Damage

Survival of corn borer larvae was the first method used as an index of plant damage or plant resistance (Caesar 1925, Painter and Ficht 1925, Neiswander et al. 1928, Houser and Huber 1929, Patch 1929, and Neiswander and Polivka 1930). In most of these early studies, experimenters relied upon natural populations for infestation. Data collected under such conditions were inconsistent, since the results obtained were dependent upon population levels and size of plants at the time of infestation. Patch and Peirce (1933), Huber (1937), and others developed methods of obtaining large quantities of corn borer egg masses so that corn plants could be uniformly infested by artificial means.

Painter (1936) indicated that the rate and extent of insect development was the only available measure of a plant's food value to an insect. Huber (1938) reported that differences in larval survival and weight were probably due to differences in the availability of plant tissues, nutritional values, or a combination of both. Patch (1943) and Dicke and Guthrie (1955) showed that growth rates of corn borer larvae were not the same on resistant and susceptible lines or hybrids. Patch reported that resistant hybrids were less suitable as food when feeding characteristics as well as weights of borers were considered. Beck and Lilly (1949) reported weights of larvae after 144 hours of feeding as an indication of the plant's food value to corn borer larvae. Bottger (1951) studied survival and weights of larvae at six different intervals up to 30 days after infestation. Beck (1956c) and George (1957) used head capsule widths as a measure of larval growth in laboratory studies. Beck reported that the head capsule widths of second instar larvae ranged from .42 mm. to .49 mm. and the average width was .46 mm.

Other methods used for evaluating corn borer resistance are concerned with the extent of damage itself. Huber (1937) counted the number of leaf punctures to determine plant resistance to first instar larvae. Dicke (1950) and Patch (1950) reported that relative resistance to early leaf feeding among strains of corn could be determined by examining the type and extent of foliar injury. Patch (1950) reported that survival was highly correlated with lesion counts in the sheath and midrib, and entrance holes into the stalk. He indicated that plant injury tended to be a better estimate of damage than survival in some experiments, since many larvae had disappeared before counts were taken and plant injuries were the only ratings which could be made. Fleming et al. (1958) used a four-class rating system in single cross studies, with one as the most resistant and four as the most susceptible. Guthrie et al. (1960) presented a nine-class system for rating inbred lines and a five-class system for rating hybrids. These systems were developed and used by F. F. Dicke in large scale experiments. The most resistant plants were assigned a value of one and plants which were the most susceptible were assigned values of nine and five. At the present time the nine-class system of rating plants for leaf-feeding damage is used by the state and federal agencies in Iowa to evaluate all plant materials for corn borer resistance.

Kwolek et al. (1958) evaluated several types of rating systems. They found that burrow counts were the least satisfactory criterion as opposed to lesion counts, larvae survival, or rating indicies. They suggested that any of the other methods evaluated could be used with satisfaction. Therefore, the choice would depend upon which one would be the most economical and biologically sound. Guthrie (1958) also found that larvae survival, leaf ratings, and lesion counts were highly correlated.

Plant Breeding

Beck (1960a) reported that by 1928 plant resistance to corn borer larvae had been established as a heritable characteristic. According to Salter et al. (1928) plant breeders and entomologists started cooperative research on the corn borer problem in 1924.

Marston and Dibble (1930) and Marston (1930a, 1930b, and 1931) reported on plant resistance studies that were conducted in Michigan with a South American type of corn called Maize Amargo. They concluded that resistance of Maize Amargo was due to a simple genetic character recessive to the susceptible Michigan varieties. Marston (1930b) proposed the use of synthetic strains to produce corn borer resistance. Meyers et al. (1937) reported that they found no indications of immunity or genetically simple resistance in their studies. They reported that resistant hybrids gave better yields than open-pollinated varieties. Patch et al. (1942) reported that inbred lines transmitted their resistance factors to hybrid combinations. These workers concluded that corn borer resistance was due to the cumulative effect of an undetermined number of multiple factors. Patch and Everly (1948) studied the inheritance of corn borer resistance in single cross and double cross combinations. They found that with higher infestations, the single crosses had smaller borer reductions than the double crosses. They also reported that a cross between a resistant line and a susceptible line had about the same effect on corn borer resistance as a cross between two partially resistant lines. Patch (1950) concluded that the genes responsible for corn borer resistance multiplied the traits of each other rather than combine additively.

Dicke and Penny (1952) reported that through extensive second-cycle breeding, recoveries which were early and resistant were obtained from crosses between early-maturing, susceptible lines and late-maturing, resistant lines. They pointed out that the degree of resistance in a double cross is dependent upon the number of resistant lines in its composition. It was suggested that three resistant lines are necessary for effective resistance and that such hybrids commonly have 50 to 60 percent less borer survival than hybrids composed of three or four susceptible lines. Holdaway (1951), Penny (1955), and Fleming et al. (1958) reported that progenies of resistant x susceptible single crosses were intermediate in reaction to corn borer damage. Penny (1955) and Fleming et al. (1958) indicated that these progenies tend more toward the resistant side and, as reported by Fleming et al., are significantly lower than the averages of both parents.

Dicke (1954) reported that our present breeding practices are directed toward obtaining resistance to the first-brood and tolerance to the second-brood. He further reported that resistance seems to be transmitted better by some lines than by others. In his studies Dicke found that satisfactory levels of resistance were not maintained beyond two backcrosses when lines such as WF9 or M14 were used as the recurrent parent. From these studies, Dicke suggested the use of two backcrosses followed by about two cycles of recombination of select plants and further backcrossing as a method of breeding for corn borer resistance. Penny (1955) also reported that all resistant lines do not transmit their resistance equally. He suggested that such differences seem to indicate that lines carry different genes or numbers of genes for resistance, and these genes are different in their dominant relationships.

As to the number of genes conditioning resistance, Penny (1955) reported that in B14 x N32, B14 x MS1, and B10 x MS1 crosses only one or two genetic factors appeared to be segregating. However, it was estimated that at least three factors were segregating in M14 x MS1 crosses, and that susceptibility was dominant. Penny (1958) reported that in the susceptible x resistant cross (WF9 x gl_7 v_{17}), resistance to early leaf feeding in gl_7 v_{17} was conditioned by a single major dominant gene, but other modifying genes may have had some influencing effects.

Ibrahim (1954) studied the number and location of genes involved in corn borer resistance by utilizing chromosomal interchanges. He reported that resistance appears as dominant in A411, and is conditioned by genes located in the long arms of chromosomes three and four and probably another in the long arm of chromosome five.

Dicke and Penny (1956) reported that the variety Lancaster Surcrop was a major source of plant resistance to young corn borer larvae of the first generation. This variety was the source of lines such as L317, R61, Oh40B, and Oh45.

Relationship of Plant Structures to Plant Resistance

Plant development was discussed briefly in the section on insect biology as an important factor of survival. Several workers reported that survival of larvae was low and insignificant on plants infested in younger stages of development, before plants were about 16 or 18 inches high.

Stages of plant development were discussed by Martin and Hershey (1935), Leng (1951), Beard and Turner (1942), and Batchelder (1949). Martin and Hershey divided plant growth into three periods -- (1) formative period; (2) period of maturity; and (3) period of pollination, fertilization, and maturation of kernels. Leng (1951) used a similar system to divide plant growth. He divided plant growth into two phases up to the time of anthesis -- (1) time when vegetative structures were forming and (2) time when reproductive structures were forming. Beard and Turner and Batchelder classified plant growth into several periods as follow: seedling, pre-whorl, early whorl, mid-whorl, late whorl, early green tassel, mid-green tassel, late green tassel, early silk, mid-silk, late silk, roasting ear, and mature ear stages.

Beard and Turner (1942) observed that plants were in the mid-whorl stage about the time that survival of corn borer larvae was improved. During this period, the tassel is rudimentary and completely enclosed in the whorl. From this and other work, Bell (1954) suggested that the transition of corn apices from producing vegetative to producing reproductive structures was the turning point in infestability of corn to corn borer larvae.

The time when transition occurs in young plants was studied by Martin and Hershey (1935), Paddick (1944), Kiesselbach (1949), Leng (1951), Bonnett (1953), and Bell (1954). Martin and Hershey reported that transition usually occurred previous to 35 days after planting. Kiesselbach reported that the tassel was evident in corn plants less than three weeks after planting. Leng indicated that the transition of eight inbred lines occurred from 25 to 31 days after planting. Batchelder (1949), Leng (1951), and Luckmann and Decker (1952) reported that the days after planting was not a good measure of when transition occurred. Leng (1951) showed that later plantings completed transition in shorter periods of time than earlier plantings. The number of visible leaves gave a good indication of internal development within but not between lines or hybrids as reported by Leng (1951). He reported that transition of the stem apices among lines which differed widely in maturity occurred when plants had from 4 to 12 visible leaves. Paddick (1944) observed a distinct tassel with the unrolling of the tenth leaf. Bonnett (1953) reported that tassel initiation in Illinois high oil line occurred after the seventh leaf was visible. Bell (1954) reported that lines WF9 and L317 had completed the vegetative phase by the time five or six leaves were visible. Tassel branches and bracts were being formed in WF9 and L317 when plants had nine and seven visible leaves, respectively.

Drake et al. (1947) observed that increased hairiness of general leaf surface seemed to hinder larval establishment and survival. Drake and Harris (1948) tested the hairiness theory and reported that this characteristic was of little value in reducing corn borer larvae, since pubescence did not develop until after the time of larval establishment.

Since corn borers usually initiate feeding on young leaf tissues, it seems reasonable to assume that leaf structures might be important in studying corn borer resistance. Prat (1948) listed and described the types of cells found on the surface of leaves. Bell (1954) studied these structures in young corn plants as they are concerned with corn borer resistance. He reported that the groups of bulliform cells on the upper surface of leaf blades were usually the initial point of attack by the first instar larvae. In studying these groups of cells for possible correlations of their composition with corn borer resistance, Bell reported that widths of bulliform groups appeared to be associated with resistance. He also reported that the bulliform cells of resistant and susceptible lines showed differential staining reactions.

MATERIALS AND METHODS

Investigations of Ten Inbred Lines

In the spring of 1959 ten inbred lines of corn with varying degrees of resistance to the European corn borer were selected on the basis of previous leaf-feeding ratings. These ten lines are listed in Table 1 with average corn borer leaf-feeding ratings. Ratings were based on a scale of one to nine with one as the most resistant and nine as the most

Table 1. Ten inbred lines of corn with average corn borer leaf-feeding ratings

Inbred line	Average corn borer rating[a]
WF9	8.5
B14	8.0
M14	7.5
B37	7.0
K150	5.0
L317	5.0
W22	5.0
Oh45	2.5
B42	2.0
CI31A	1.5

[a]Ratings were based on a scale of 1 to 9 with 1 as the most resistant and 9 as the most susceptible. These ratings were furnished by F. F. Dicke of the European Corn Borer Research Laboratory at Ankeny, Iowa in 1962 in a personal communication.

susceptible. These ratings were furnished by F. F. Dicke of the European Corn Borer Research Laboratory at Ankeny, Iowa in 1962 in a personal communication. Average leaf-feeding ratings indicate the general performance of these lines over several years of testing.

Field infestations

The ten inbred lines were planted in the field in 1959, 1960, and 1961, using a randomized complete block design with four replications. In 1959 six to ten plants were selected at random on each of three dates, 14, 17, and 19 days after 50 percent of the plants had emerged from the soil. Selected plants were infested with two average sized corn borer egg masses in the blackhead stage. These egg masses were pinned to the upper surface of the largest whorl leaf close to the whorl region. One half of the plants were dissected five days after plants were infested and the other half were dissected ten days after plants were infested. These plant dissections were referred to as the five and ten day counts. The number of larvae which survived on each plant was recorded and an average number of larvae per plant was calculated for each plot on the three dates of infestation. These average survival data were transformed using the square root of X plus one ($\sqrt{X \quad 1}$) and analysed by analyses of variance. The square root transformation was used because the raw data are enumeration data which tend to follow a Poisson distribution. In a Poisson distribution the variance is proportional to the mean and effects are non-additive (Snedecor 1956).

The number of visible leaves was recorded for each plant infested as an indication of plant development on dates of infestation. A sample of ten stem apices was also collected from each plot on the dates of infestation. These samples were preserved by freezing until such time that they could be dissected and examined to determine when transition occurred. Stem apices in vegetative, transition, and floral stages of development are illustrated in Figures 1, 2, 3, and 4. When the frozen stem apices were examined, all apices in the vegetative stage were assigned a value of one, those in transition were assigned a value of two, and those in the floral stage were assigned a value of three. Average values were calculated for the apical development of each line on the three dates of infestation.

In 1960 the ten inbred lines were infested in the field on five dates -- 10, 11, 12, 13, and 15 days after 50 percent of the plants emerged from the soil -- by the same methods used in 1959 studies. Five and ten day counts were made and the transformed data ($\sqrt{X\ \ 1}$) were analysed by analyses of variance. The number of visible leaves was recorded for each plant infested, as a measure of plant growth.

In 1961 infestations were made 4, 6, 8, 10, 12, and 14 days after plant emergence. However, only three to six plants were infested in each plot and only the five day counts were observed. Numbers of visible leaves were recorded for all infested plants. The transformed survival data ($\sqrt{X\ \ 1}$) were analysed by analysis of variance.

In addition to recording total numbers of larvae per plant in 1961, each plant was divided into three areas (low, whorl, and exposed leaf) and the number of larvae in each area was recorded. These three plant areas are illustrated in Figure 5. Those larvae which were found at the base of the plant or behind the leaf sheaths of leaves with exposed ligules

Figure 1. Vegetative stem apex of a corn plant that had 4 visible leaves. X85

Figure 2. Stem apex in the stretch phase, early transition, of a corn plant that had 5 visible leaves. X85

Figure 3. Stem apex, transition stage, of a corn plant that had 5 visible leaves. X85

Figure 4. Stem apex, early floral stage, of an M14 corn plant that had 7 visible leaves. X85

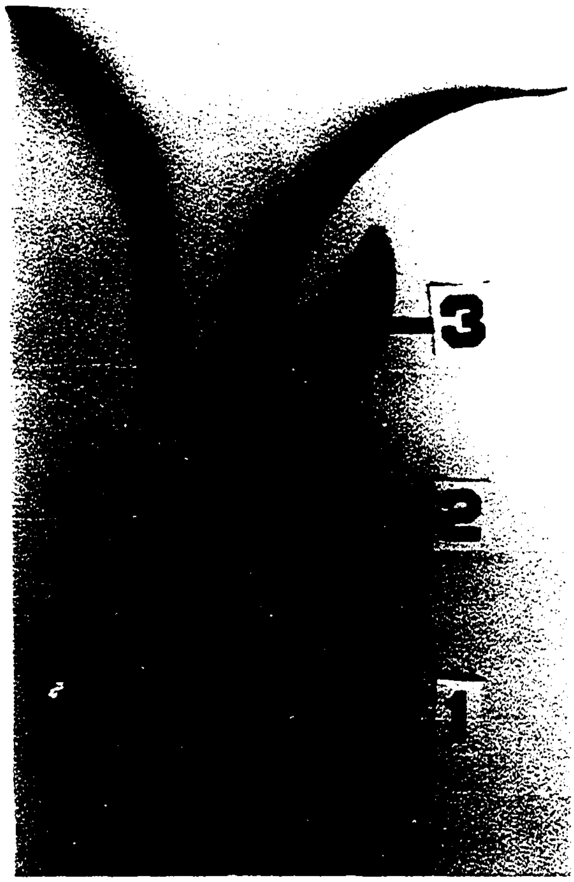

Figure 5. Young corn plant divided into three areas (low -- 1, whorl -- 2, and exposed leaf -- 3) as used for recording the positions of larvae on plants in the 1961 field studies.

were included in the low area. Those larvae found in the rolled leaves near the moist area were considered as being in the whorl area and all other larvae were considered as being in the exposed leaf area. Total numbers of larvae which survived across all dates of infestation in the three plant areas were calculated for all four replications of each line. These survival data were transformed by square root and analysed by analyses of variance.

Laboratory infestations

Since survival and growth of newly hatched corn borer larvae are closely associated with temperature and moisture conditions, it seemed reasonable that mortality rates might be decreased if these conditions were controlled. Preliminary studies were conducted in the early spring of 1960 to determine if survival rates of newly hatched larvae might be increased and line differences maintained in the laboratory under controlled temperature and humidity conditions. Results of these studies indicated that survival rates were improved for each of the two lines used, CI31A and WF9. It appeared that about twice as many larvae could survive on WF9 as on CI31A in these studies.

During the 1960 growing season three plants were selected at random from each of three field replications on nine dates, between 2 and 16 days after 50 percent of the plants emerged from the soil. The selected plants were taken to the laboratory where numbers of visible leaves were recorded and whorl sections were removed for infestation. It was necessary to dry the plants for about 30 minutes to eliminate excess moisture before the whorl sections were removed and infested. Figure 6 illus-

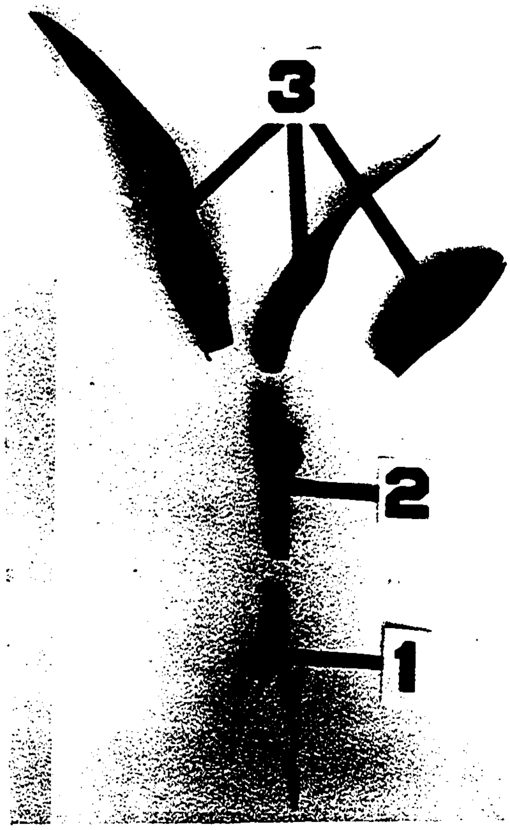

Figure 6. Young corn plant illustrating the method of trimming whorl sections (plant part 2) for the laboratory studies. Plant parts 1 and 3 were discarded.

trates the method used to remove the whorl sections (plant part 2) from small plants. Those plant parts which were labeled 1 and 3 in Figure 6 were discarded. Each whorl section was placed in a test tube with an egg mass which contained from 13 to 39 blackhead eggs. The test tubes were plugged with cellucotton so that larvae could not escape and were placed in a constant temperature and humidity chamber set at 76° F. and 78 percent relative humidity. Larvae were left in this environment for five days after which the whorl sections were dissected and the number of surviving larvae recorded. Previous studies showed that larvae could not survive for five days under these conditions without feeding on plant materials.

Average survival percentages were calculated by dividing the total number of surviving larvae by the total number of eggs applied to the three plants from each replication. These survival percentages were transformed using the arcsin transformation and tested by analysis of variance. Snedecor (1956) reported that the arcsin transformation of percentage data, which tends to follow a binomial distribution, gives more weight to the smaller percentages which have smaller variations.

All surviving larvae were preserved in 70 percent alcohol so that the stage of larval growth could be measured at a later time. Examination of the preserved larvae indicated that some larvae had reached the second instar after five days of feeding in the laboratory. Stages of larval growth were determined by measuring head capsule widths. All larvae with head capsule widths of .22 mm. to .32 mm. were considered first instar larvae and all with widths of .41 mm. to .56 mm. were considered second instar larvae. Numbers of second instar larvae were recorded for each line on all nine dates of infestation. From these numbers average percentages of second instar larvae were calculated as measures of larval growth. Two values were calculated for each line, the first by dividing the total number of second instar larvae by the total number of larvae which survived, and the second by dividing the total number of second instar larvae by the total number of eggs applied to each line.

Preliminary studies were conducted in the early spring of 1961 to determine the most effective number of eggs to use for laboratory infestations. Results of these studies indicated that 15 to 25 eggs were sufficient to measure differences between lines. The analysis of variance of the transformed data and a graphic illustration of survival percentages are presented in the appendix (Table 37 and Figure 17) for these preliminary studies.

The laboratory studies of corn borer survival on the ten inbred lines were repeated in 1961. However, only two plants were taken from each of three replications and infestations were made on only seven dates. Dates of infestation were two days apart, starting on the second day after plant emergence. Procedures were improved somewhat in 1961, in that plants were dried until the leaves had started to wilt before whorl sections were removed and placed in the test tubes. This tended to remove excess moisture and helped to decrease the rate of plant decomposition. Each plant sample was infested with an egg mass consisting of from 13 to 25 eggs in the blackhead stage. All other procedures were the same as described in the 1960 Laboratory studies.

Investigations of Six Single Crosses

In 1961 six single crosses involving some of the ten inbred lines were selected for their reaction to corn borer leaf feeding. These single crosses are listed in Table 2 with their average corn borer leaf-feeding ratings. These ratings were supplied by F. F. Dicke of the European Corn Borer Research Laboratory at Ankeny, Iowa in 1962 in a personal communication. Three groups of single crosses were included in these studies; two susceptible x susceptible, two resistant x susceptible, and two resistant x resistant.

Field infestations

The six single crosses were planted in a separate experiment in the field in 1961 using a randomized complete block design with four replica-

Table 2. Six single crosses with average corn borer leaf-feeding ratings

Single cross	Average corn borer rating[a]
B37 X WF9	8.0
M14 X WF9	8.0
B42 X WF9	4.5
CI31A X WF9	3.5
B42 X W22	3.0
CI31A X Oh45	2.0

[a]Ratings were based on a scale of 1 to 9 with 1 as the most resistant and 9 as the most susceptible. These ratings were furnished by F. F. Dicke of the European Corn Borer Research Laboratory at Ankeny, Iowa in 1962 in a personal communication.

tions. Three to six plants were selected at random and infested with two average sized blackhead egg masses on six dates. Dates of infestation were two days apart, starting on the second day after 50 percent of the plants emerged from the soil. The number of visible leaves was recorded for each plant infested as a measure of plant development. All infested plants were dissected five days after eggs were applied and numbers of surviving larvae were recorded. The average number of larvae per plant was calculated for each plot for each of the six dates of infestation. These survival data were transformed by the square root transformation $(\sqrt{X \quad 1})$ and analysed by analysis of variance.

In addition to recording total survival of larvae per plant, each plant was divided into low, whorl, and exposed leaf areas as illustrated in Figure 5 and survival in each area was recorded. Survival of larvae in the plant areas of each single cross was totaled for each replication and these data were transformed by square root of X plus one $(\sqrt{X \quad 1})$ and analysed by analyses of variance.

Laboratory infestations

Plants were removed from the field plots of the six single crosses on seven dates and infested in the laboratory, applying the same procedures used for the laboratory studies of the ten inbred lines in 1961.

Investigations of Six Related Inbred Lines

Corn borer survival was studied on a third group of plant material in 1961. This group of material included WF9 and five closely related inbred lines which were recovered from the following cross:

$$\left[(\mathrm{K114} \times \mathrm{WF9}^{(3)}) \times (\mathrm{41.2504B} \times \mathrm{WF9}^{(3)})\right]$$

These five lines are theoretically about 75 percent WF9 type. They were selected for this study on the basis of two previous years of corn borer leaf-feeding ratings. The six related inbred lines are listed in Table 3 with average leaf-feeding ratings. Line numbers presented here are entry or row numbers from the 1960 planting.

Field infestations

Two sources of seed for each line were obtained from 1960 selections and these were planted in the field in 1961 using a randomized complete block design with two replications. The two seed sources were utilized as subplots. Plants were infested in the field, and survival data were collected and analysed by the same methods described for the ten inbred

Table 3. Six related inbred lines with average corn borer leaf-feeding ratings over three years

Inbred line	Corn borer rating[a]			
	Average for year			Three year average
	1959	1960	1961	
WF9	----	----	8.50	8.50
1406	5.00	5.00	7.00	5.67
1412	3.00	5.00	4.75	4.25
1400	3.00	3.00	4.50	3.50
1426	4.00	3.00	2.50	3.17
1405	2.00	2.00	2.75	2.25

[a]Ratings were based on a scale of 1 to 9 with 1 as the most resistant and 9 as the most susceptible.

lines and six single crosses in 1961.

Laboratory infestations

Corn borer survival and larval growth were studied in the laboratory using whorl sections from the six related inbred lines. The methods employed were the same as those described for the ten inbred lines and the six single crosses in 1961.

Arrangement of Leaf Structures

Since Bell (1954) reported that the bulliform groups were usually the initial points of corn borer attack on young plants, there has been an interest in the relationship of these corn leaf structures to corn borer resistance. Several characteristics of the arrangement of bulliform groups were studied for their possible relationship to corn borer resistance. Characteristics studied included the area of leaf per bulliform hair, the distance between bulliform hairs along bulliform groups, the distance between bulliform groups across the sample area of the leaf, and the width of bulliform groups. These characteristics were studied among the ten inbred lines, the six single crosses, and the six related inbred lines.

All arrangements of corn leaf structures were studied on mature leaves, at a uniform position, which were collected from plants on the dates of silking. The blade of the leaf which subtends the developing ear was sampled at the widest and most fully expanded part. Silking dates were used so that plants would be in a more or less uniform stage of plant growth. Each sample consisted of about 15 to 20 small pieces each of two different shapes, approximately 4 mm. long x 2 mm. wide and 2 mm. long x

10 mm. wide. These were cut from each of three plants per line or single cross. The samples were preserved in FAA and later were transferred to a 50 percent glycerin-alcohol mixture. This treatment tended to clear the sections slightly so that they could be examined with the aid of a microscope using transmitted light.

Ten pieces of leaf were selected at random from each sample -- five pieces of each shape. These selected pieces were used to estimate the area of leaf per bulliform hair, the distance between bulliform hairs along bulliform groups, and the distance between bulliform groups across the leaf samples. The selected pieces, still in glycerine-alcohol, were placed on a slide so that the bulliform groups were on the upper surface. A cover slip was applied and measurements were made with an eye-piece micrometer. The number of bulliform hairs and the number of bulliform groups were counted on each leaf piece.

Calculations for measuring the area of leaf per bulliform hair were made by determining the total surface area of all five pieces in each sample shape and dividing this total by the number of bulliform hairs found on these same pieces. The distance between bulliform hairs was calculated by multiplying the number of bulliform groups across each leaf piece by the length of the leaf piece, summing all five pieces per sample, and dividing this total by the number of bulliform hairs found on all five pieces. The distance between bulliform groups was estimated by dividing the total width of all five pieces by the total number of bulliform groups on these leaf pieces. Differences among lines or single crosses and between shapes of leaf pieces were tested for each of these characteristics by analyses of variance.

One other characteristic, width of bulliform groups, was studied also. Bell (1954) suggested a possible correlation between this characteristic and corn borer resistance. In the present study, the widths of bulliform groups were determined from samples of five of the wide leaf pieces described above. Five bulliform groups were measured on each leaf piece with an ocular micrometer. Average widths of bulliform groups among the lines or single crosses and leaf pieces were analysed by analyses of variance.

RESULTS

Investigations of Ten Inbred Lines

Field infestations

Survival of larvae   Survival of European corn borer larvae was not the same on each of ten inbred lines when tested in the field in 1959, 1960, and 1961. Mean numbers of corn borer larvae which survived for five days in 1959, 1960, and 1961 and ten days in 1959 and 1960 are presented in Table 4. Significant differences among the ten inbred lines for survival of larvae were observed at the one percent level of probability when the transformed data were analysed by analyses of variance (Tables 5, 6, 7, and 8). The transformed means for each experiment were ranked and Duncan's New Multiple Range Test (Duncan 1955) was used to test each mean with every other mean. The results of this test are presented in Table 9. The Duncan's test allows for the wider differences required for significance when means further apart in rank are compared.

Each set of five or ten day survival means presented in Table 4 was correlated with the average corn borer leaf-feeding ratings and the correlations for survival of larvae with corn borer leaf-feeding ratings were significant at the one percent level of probability except the five day counts of 1960 and this was significant at the five percent level.

Differences between survival of larvae at the five and ten day counts for 1959 and 1960 in terms of number of larvae and percent reduction after five days are presented in Table 4. These differences indicate the mortality of five to ten day old larvae. In general, those lines which had the highest survivals at the five day counts had the largest reductions in

Table 4. Mean numbers of European corn borer larvae which survived on the ten inbred lines in 1959, 1960, and 1961 with differences between the five and ten day counts and simple correlation coefficients (r values) for survival with average corn borer leaf-feeding ratings

Inbred line	Average corn borer rating	Mean survival of larvae per plant (number or percent)								
		1959				1960				1961
		Survival		Difference		Survival		Difference		
		5 day	10 day	Number	Percent	5 day	10 day	Number	Percent	5 day
WF9	8.5	4.15	2.39	1.76	42.4	1.92	1.37	.55	28.6	3.58
B14	8.0	3.08	1.10	1.98	64.3	2.20	1.28	.92	41.8	2.35
M14	7.5	4.29	2.46	1.83	42.7	1.66	1.34	.32	23.9	2.03
B37	7.0	3.62	2.72	.90	24.9	2.17	1.72	.45	20.7	2.80
K150	5.0	3.24	.93	2.31	71.3	3.16	1.72	1.44	45.6	3.16
L317	5.0	1.43	.80	.63	44.1	.54	.44	.10	18.5	.96
W22	5.0	1.92	1.04	.88	45.8	.66	.28	.38	57.6	.88
Oh45	2.5	1.96	.61	1.35	68.9	.64	.14	.50	78.1	1.07
B42	2.0	.74	.44	.30	40.5	.28	.25	.03	10.7	.76
CI31A	1.5	.32	.08	.24	75.0	.23	.21	.02	8.7	.37
Average survival		2.48	1.26	1.22	49.2	1.35	.88	.47	34.8	1.80
Simple r value		.887**	.828**	----	----	.686*	.776**	----	----	.784**

*Correlation significant at the 5 percent level of probability.

**Correlation significant at the 1 percent level of probability.

Table 5. Analyses of variance for survival of European corn borer larvae on young corn plants of ten inbred lines infested in the field in 1959

Source of variation	Degrees of freedom	Mean square	F value
		Total of 5 and 10 day counts[a]	
Replications	3	.012	.175
Lines	9	2.785	40.020**
Error a	27	.070	
Dates	2	11.562	58.688**
Error b	6	.197	
Lines x Dates	18	.341	4.983**
Error c	54	.068	
Counts	1	7.378	92.456**
Lines x Counts	9	.217	2.719**
Dates x Counts	2	.827	10.361**
Lines x Dates x Counts	18	.039	.489
Error d	90	.080	
		5 day counts[b]	
Replications	3	.021	.276
Lines	9	1.906	24.959**
Error a	27	.076	
Dates	2	9.268	35.811**
Linear Regression	1	14.460	60.961**
Quadratic Regression	1	4.076	15.750**
Error b	6	.259	
Lines x Dates	18	.237	2.844**
Error c	54	.083	
		10 day counts[c]	
Replications	3	.018	.187
Lines	9	1.097	11.459**
Error a	27	.096	
Dates	2	3.120	94.558**
Linear Regression	1	6.034	182.858**
Quadratic Regression	1	.207	6.258*
Error b	6	.033	
Lines x Dates	18	.142	2.603**
Error c	54	.055	

[a]Coefficient of variation was 17.12 percent.

[b]Coefficient of variation was 15.82 percent.

[c]Coefficient of variation was 15.90 percent.

*Significant differences at the 5 percent level of probability.

**Significant differences at the 1 percent level of probability.

Table 6. Analyses of variance for survival of European corn borer larvae on young plants of ten inbred lines infested in the field in 1960

Source of variation	Degrees of freedom	Mean square	F value
	Total of 5 and 10 day counts[a]		
Replications	3	.630	5.751**
Lines	9	3.169	28.913**
Error a	27	.110	
Dates	4	1.607	12.545**
Error b	12	.128	
Lines x Dates	36	.087	1.811**
Error c	108	.048	
Counts	1	2.174	63.757**
Lines x Counts	9	.152	4.455**
Dates x Counts	4	.769	22.551**
Lines x Dates x Counts	36	.057	1.663*
Error d	150	.034	
	5 day counts[b]		
Replications	3	.412	4.601**
Lines	9	2.137	23.879**
Error a	27	.090	
Dates	4	2.212	23.859**
Linear Regression	1	8.053	86.866**
Quadratic Regression	1	.667	7.191*
Deviations	2	.064	.688
Error b	12	.093	
Lines x Dates	36	.107	2.176**
Error c	108	.049	
	10 day counts[c]		
Replications	3	.251	4.594**
Lines	9	1.184	21.640**
Error a	27	.055	
Dates	4	.164	2.663
Linear Regression	1	.505	8.177*
Quadratic Regression	1	.117	1.895
Deviations	2	.018	.290
Error b	12	.062	
Lines x Dates	36	.033	.938
Error c	108	.035	

[a]Coefficient of variation was 12.98 percent.

[b]Coefficient of variation was 14.79 percent.

[c]Coefficient of variation was 13.94 percent.

*Significant differences at the 5 percent level of probability.

**Significant differences at the 1 percent level of probability.

Table 7. Analysis of variance for survival of European corn borer larvae on young corn plants of ten inbred lines infested in the field in 1961[a]

Source of variation	Degrees of freedom	Mean square	F value
Replications	3	.116	.892
Lines	9	2.777	21.427**
Error a	27	.130	
Dates	5	2.072	35.721**
Linear Regression	1	8.587	148.052**
Quadratic Regression	1	1.483	25.576**
Deviations	3	.096	1.660
Error b	15	.058	
Lines x Dates	45	.090	1.320
Error c	135	.068	

[a]Coefficient of variation was 15.88 percent.

**Significant differences at the 1 percent level of probability.

Table 8. Combined analysis of variance for survival of European corn borer larvae after five days of feeding on young corn plants of ten inbred lines in the years 1959, 1960, and 1961[a]

Source of variation	Degrees of freedom	Mean square	F value
Years	2	1.079	49.500**
Replications within Years	9	.037	1.674
Lines	9	1.401	23.200**
Years x Lines	18	.060	2.771**
Replications within Years x Lines	81	.022	

[a]Coefficient of variation was 8.92 percent.

**Significant differences at the 1 percent level of probability.

Table 9. Ranked transformed[a] means for survival of European corn borer larvae in the field for ten inbred lines with Duncan's New Multiple Range Test applied[b]

1959 (5 day counts)

CI31A	B42	L317	W22	Oh45	B14	K150	B37	WF9	M14
1.15	1.32	1.56	1.71	1.72	2.02	2.06	2.15	2.27	2.30

1959 (10 day counts)

CI31A	B42	Oh45	L317	K150	W22	B14	WF9	M14	B37
1.04	1.20	1.27	1.34	1.39	1.43	1.45	1.84	1.86	1.93

1960 (5 day counts)

CI31A	B42	L317	Oh45	W22	M14	WF9	B37	B14	K150
1.11	1.13	1.24	1.28	1.29	1.63	1.71	1.78	1.79	2.04

1960 (10 day counts)

Oh45	CI31A	B42	W22	L317	B14	M14	WF9	K150	B37
1.07	1.10	1.12	1.13	1.20	1.51	1.53	1.54	1.65	1.65

1961 (5 day counts)

CI31A	B42	W22	L317	Oh45	M14	B14	B37	K150	WF9
1.17	1.33	1.37	1.40	1.44	1.74	1.83	1.95	2.04	2.14

[a]Transformed by the square root of X plus one ($\sqrt{X+1}$).

[b]Any two means which are underscored by the same line are not significantly different at the 1 percent level of probability.

number of larvae by the ten day counts, and those with the lowest survivals at five days had the smallest reductions in number of larvae by the ten day counts. When average percentages were compared for the reduction of larvae between the five and ten day counts, three lines (B14, K150, and Oh45) seemed to give larger reductions for both years tested. Two other lines (W22 and CI31A) had comparatively large percent reductions for either one year or the other. The consistency for larger reductions of larvae between the five and ten day counts on the three lines seems to indicate that the factor or factors which cause mortality of five to ten day old larvae on young corn plants might be different among lines. The five day survivals on K150 tended to be higher than expected on the basis of the average leaf-feeding ratings of older plants.

Differences of larval survival between the five and ten day counts were highly significant at the one percent level of probability for both years as indicated in the analyses of variance (Tables 5 and 6). Since the five and ten day counts were different, each was analysed in a separate analysis of variance. The analyses of variance for the five and ten day counts of 1959 and 1960 are presented in Tables 5 and 6.

Age of corn plants at the time of infestation tended to influence the number of corn borer larvae which survived on each line. The average tendency for larger numbers of larvae to survive on older plants of the ten inbred lines was observed for both five and ten day counts in 1959 and 1960 (Figures 7 and 8) and for the five day counts in 1961 (Figure 9). Ages of corn plants as presented in these figures were measured on the basis of days after plant emergence. Differences in survival of corn borer larvae on the various dates of infestation were tested by analyses

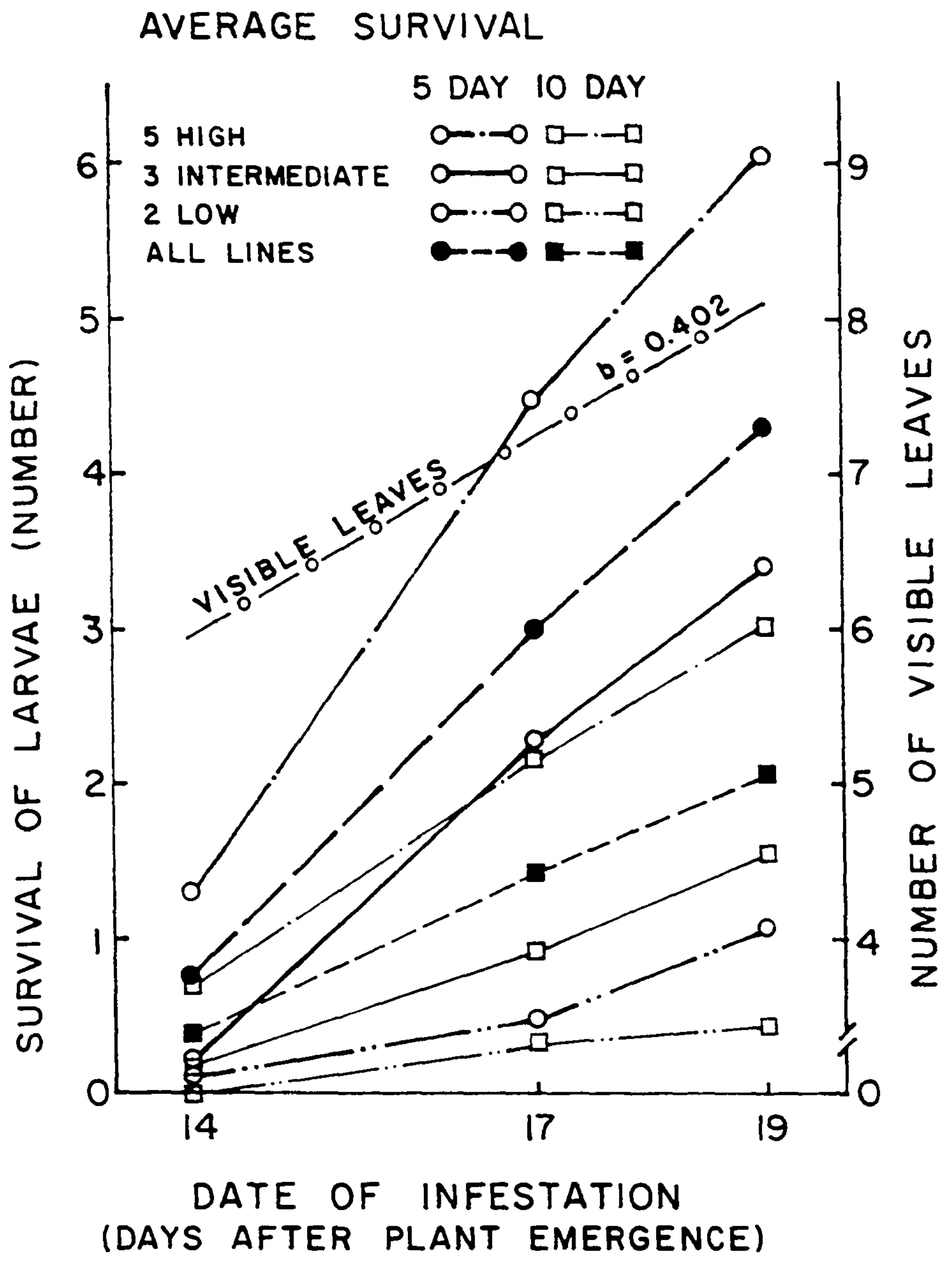

Figure 7. Average survival patterns of European corn borer larvae after five and ten days of feeding on young plants of ten inbred lines infested in the field in 1959

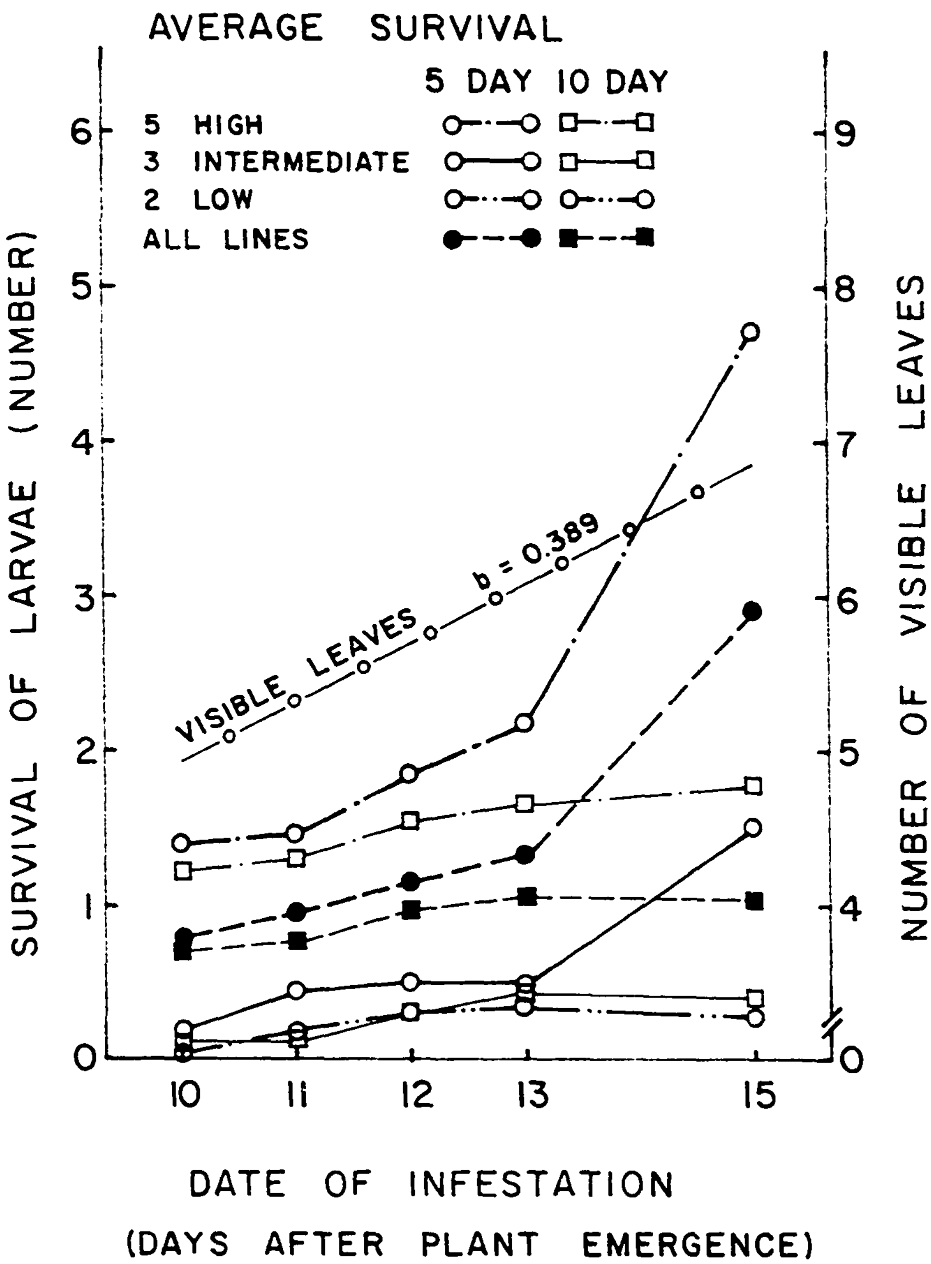

Figure 8. Average survival patterns of European corn borer larvae after five and ten days of feeding on young plants of ten inbred lines infested in the field in 1960

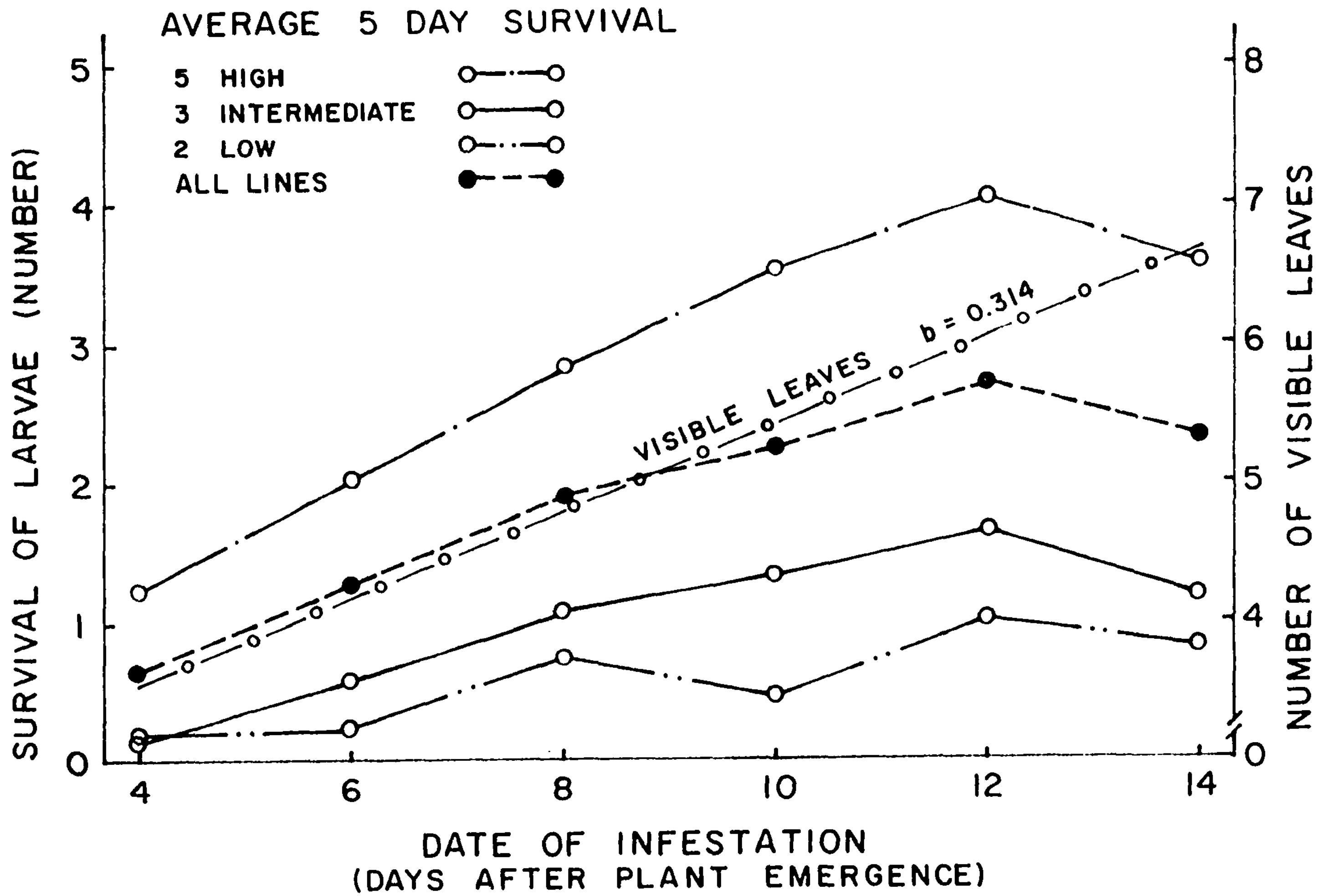

Figure 9. Average survival patterns of European corn borer larvae after five days of feeding on young plants of ten inbred lines infested in the field in 1961

of variance and the results are presented in Tables 5, 6, and 7. Mean squares for dates of infestation were significant at the one percent level of probability for five day counts in all three years and for the ten day counts in 1959. The analysis of variance for the ten day counts in 1960 (Table 6) indicated that survival levels for dates of infestation were not significantly different; however, the linear component for dates was significant at the five percent level. The linear and quadratic components accounted for most of the variation among the dates of infestation for all field experiments of the ten inbred lines (Tables 5, 6, and 7).

The ten inbred lines were arranged into three groups with regard to the number of larvae which survived on them. Five inbreds (WF9, B14, M14, B37, and K150) were grouped together as lines with high survival, three inbreds (L317, W22, and Oh45) were grouped as lines with intermediate survival, and the other two (B42 and CI31A) were grouped as lines with low survival. Group survival means are presented in Figures 7, 8, and 9 for five and ten day counts on the dates of infestation. The five and ten day counts of the low group were not greatly different in 1960, therefore, they were averaged together in Figure 9.

Mean squares for the lines x dates interactions were significant at the one percent level of probability in the five and ten day counts of 1959 and the five day counts of 1960, but were not significant at the five percent level in the ten day counts of 1960 or the five day counts of 1961. However, the five day counts of 1961 were significant at the ten percent level. A significant interaction of lines x dates indicated that all lines did not react the same across dates of infestation. Differences in survival of young larvae among the inbred lines tended to be smaller on younger plants and larger on older plants. This pattern for survival of larvae is illustrated in Figure 7 for both the five and ten day counts of 1959 and Figures 8 and 9 for the five day counts of 1960 and 1961 where means for the three survival groups are presented. The group survival means of the ten day counts in 1960 (Figure 8) did not follow this same pattern, but instead, tended to parallel each other.

Lines x counts interactions were significant at the one percent level of probability for both 1959 and 1960. This indicated that reductions in number of larvae between the five and ten day counts were not the same for all lines. The dates x counts interactions were also significant at the one percent level for both years which indicated that differences in survival between the five and ten day counts were not the same on the various dates of infestation. The threeway interaction for lines x dates x counts was not significant in 1959, but was significant at the five percent level of probability in 1960.

Survival means for the five day counts in all three years were combined into an analysis of variance (Table 8). Survival rates were different among the years as indicated by the significant mean square for years. The interaction of years x lines was also significant which indicated that relative positions of lines were not the same in all years.

The average number of visible leaves per plant, which was used as a measure of plant growth, tended to increase by about 0.3 to 0.4 per day for the ten lines up to 19 days after plant emergence. This pattern was observed during all three years. Linear regression lines for number of visible leaves on dates of infestation are presented in Figures 7, 8, and 9 for 1959, 1960, and 1961, respectively.

<u>Plant transition of stem apices</u> Results of the transition studies for ten inbred lines indicated that all lines do not enter transition at the same stage of plant development, nor do they progress at the same rates. The transition stages of stem apices are illustrated in Figures 1, 2, 3, and 4. Sizes of plants in terms of estimated numbers of visible leaves are presented in Table 10 for the times when corn stem apices enter

Table 10. Estimated average numbers of visible leaves[a] at the time of floral initiation of the stem apices for ten inbred lines

Inbred line	Number of visible leaves at start	Number of visible leaves at completion
WF9	6.7	9.0
B14	7.1	9.4
M14	5.5	7.3
B37	5.6	7.7
K150	6.4	9.5
L317	4.5	9.5
W22	6.2	9.6
Oh45	6.3	9.0
B42	5.9	9.3
CI31A	6.2	10.3
Average	6.0	9.1

[a]Estimated average numbers of visible leaves were made on the assumption that floral transition and number of visible leaves were both linear or near linear across dates. That is, when floral initiation was started it continued at about the same rate until completion and new visible leaves were added at a rather constant rate.

and complete transition from vegetative to floral stages. These estimates were calculated from data collected in 1959. The relationships of stem apex determinations and numbers of visible leaves were nearly linear across the three dates of infestation. In other words, plants produced visible leaves at a rather constant rate, and once floral transition was initiated it continued at about the same rate until completion. From data presented in Table 10 it was evident that all lines did not enter or complete transition when the same number of visible leaves were present. In general, most lines entered transition when plants had an average of six visible leaves and completed transition when plants had an average of nine visible leaves. Line L317 had the lowest number of visible leaves with an average of 4.5 when plants entered transition, and B14 had the highest number with an average of 7.1 visible leaves. M14 and B37 had the lowest numbers of visible leaves when transition was completed with 7.3 and 7.7, respectively, while CI31A had the highest with 10.3 visible leaves. According to these data most lines completed transition before 9.5 leaves were visible. It appeared that resistance to early corn borer survival on young corn plants was not directly related to apical transition, but rather was a function of plant age, measured in days after plant emergence. This was indicated by the significant differences which were observed among the lines when plants were infested up through the transition stage.

<u>Location of larvae</u> In 1961 each plant dissected was divided into three areas (low, whorl, and exposed leaf) and the number of larvae in each area recorded. Patterns for survival of larvae were observed among the lines over the four replications. The average numbers and percentages of larvae found in each area after five days of feeding on the ten lines

are presented in Table 11. Average numbers of larvae in each plant area were transformed using the square root transformation ($\sqrt{X \quad 1}$) and analysed by analyses of variance (Table 12). Since the mean squares for areas and lines x areas were significant, survival in each area was analysed separately to test differences among lines. From these analyses it was observed that survival levels of the lines were significantly different at the one percent level of probability in the low and whorl areas and significantly different at the five percent level in the exposed leaf area.

Table 11. Average survival of European corn borer larvae in numbers and percentages for three areas of young corn plants of ten inbred lines in 1961

Inbred line	Plant area: Low		Whorl		Exposed leaf		Total survival
	Number	Percent	Number	Percent	Number	Percent	
WF9	1.25	31.56	2.48	62.63	.23	5.81	3.96
B14	.97	36.60	1.46	55.10	.22	8.30	2.65
M14	.54	24.32	1.39	62.61	.29	13.06	2.22
B37	.71	23.13	2.21	71.98	.15	4.89	3.07
K150	.57	16.15	2.60	73.65	.36	10.20	3.53
L317	.29	25.00	.59	50.86	.28	24.14	1.16
W22	.48	47.53	.39	38.61	.14	13.86	1.01
Oh45	.79	62.70	.40	31.75	.07	5.55	1.26
B42	.46	48.94	.28	29.79	.20	21.27	.94
CI31A	.13	30.95	.21	50.00	.08	19.05	.42

Table 12. Analyses of variance for survival of European corn borer larvae in three plant areas of ten inbred lines in 1961

Source of variation	Degrees of freedom	Mean square	F value
	Total for all three areas[a]		
Replications	3	.192	.265
Lines	9	14.258	19.650**
Error a	27	.726	
Areas	2	75.573	194.027**
Lines x Areas	18	5.356	13.752**
Error b	60	.390	
	Low area[b]		
Replications	3	.188	.414
Lines	9	4.381	9.631**
Error	27	.455	
	Whorl area[c]		
Replications	3	.595	.837
Lines	9	19.634	27.626**
Error	27	.711	
	Exposed leaf area[d]		
Replications	3	.054	.153
Lines	9	.955	2.699*
Error	27	.354	

[a]Coefficient of variation was 16.47 percent.

[b]Coefficient of variation was 17.32 percent.

[c]Coefficient of variation was 16.51 percent.

[d]Coefficient of variation was 25.16 percent.

*Significant differences at the 5 percent level of probability.

**Significant differences at the 1 percent level of probability.

In general, significantly more larvae were found in the whorl than in either low or exposed leaf areas, and significantly more were found in the low area than on the exposed leaf area. All lines did not have the same proportions of larvae in each area, but rather, each line seemed to follow a definite pattern. For example, WF9 had an average of 3.96 larvae per plant of which 31.56 percent were in the low area, 62.63 percent were in the whorl area, and 5.81 percent were on the exposed leaf area; and Oh45 had 1.26 larvae per plant of which 62.70 percent were in the low area, 31.75 percent were in the whorl area, and 5.55 percent were on the exposed leaf area.

Laboratory infestations

Differences in the survival and growth of corn borer larvae were observed in the whorl area of ten inbred lines when tested in the laboratory under controlled temperature and humidity conditions. Average percent survival and larval growth in terms of percentages of second instar larvae are presented in Table 13. Two values are presented for percent of second instar larvae; one was calculated by dividing the total number of second instar larvae into the total number of larvae which survived on each line, and the other was calculated by dividing the total number of second instar larvae into the total number of eggs applied to each line.

Each set of survival and growth data presented in Table 13 was correlated with the average corn borer leaf-feeding ratings. In addition to these simple correlations, multiple correlations were calculated each year for survival percentages and percentages of second instar larvae of those which survived with the average corn borer leaf-feeding ratings. Simple

Table 13. Average survival and growth of European corn borer larvae in the whorl areas of ten inbred lines tested in the laboratory in 1960 and 1961 with simple and multiple correlation coefficients (r and R values)

Inbred line	Average corn borer rating	1960 Percent survival	1960 Percent second instar[a]	1960 Percent second instar[b]	1961 Percent survival	1961 Percent second instar[a]	1961 Percent second instar[b]
WF9	8.5	38.26	57.91	22.15	43.70	49.58	21.66
B14	8.0	20.99	42.01	8.82	37.87	58.82	22.28
M14	7.5	30.51	51.98	15.86	37.47	37.88	14.19
B37	7.0	30.45	58.47	17.80	34.68	50.91	17.65
K150	5.0	22.08	53.17	11.74	34.16	39.64	13.54
L317	5.0	21.53	23.24	5.00	21.66	27.91	6.05
W22	5.0	15.11	27.69	4.18	25.34	18.63	4.72
Oh45	2.5	22.12	38.08	8.42	31.18	29.23	9.11
B42	2.0	22.84	24.19	5.52	27.52	25.34	6.97
CI31A	1.5	15.66	15.13	2.37	22.79	11.83	2.70
Averages		23.96	39.19	10.19	31.64	34.98	11.89
Simple r value[c]		.655*	.756*	.751*	.761*	.827**	.889**
Multiple R value[d]		----	.763*	----	----	.835**	----

[a]Percent of second instar larvae of those which survived.

[b]Percent of second instar larvae of the total eggs applied.

[c]Simple correlation of survival or larval growth with average corn borer leaf-feeding ratings.

[d]Multiple correlation of percent survival plus percent of second instar larvae of those which survived with average corn borer leaf-feeding ratings.

*Correlation significant at the 5 percent level of probability.

**Correlation significant at the 1 percent level of probability.

and multiple correlation coefficients are presented at the bottom of Table 13. All correlations were significant at either the one or five percent levels of probability. Correlation coefficients ranged from 0.655 to 0.889. Larval growth values tended to give higher correlations than survival values.

Survival differences among the lines were significant at the one percent level of probability as indicated by the analysis of variance (Table 14). Arcsin transformed means were ranked and Duncan's New Multiple Range Test (Duncan 1955) was used to test differences between means (Table 15).

Average survivals of larvae in the laboratory studies were different on the dates of infestation. Mean squares for dates were significant at the one percent level of probability in both years. The variation among dates was broken down into linear and quadratic components plus deviations from linear and quadratic. The linear component accounted for most of the variation among dates in both years. More larvae were able to survive on plants which were infested on the later dates. Survival of larvae on the various dates of infestation in 1961 was more consistent than in 1960. This was probably due to improved methods of handling plant samples in the 1961 studies.

The mean squares for the lines x dates were not significant in either year which indicated that the relative positions of lines were not greatly different for the dates of infestation.

Mean survival percentages for 1960 and 1961 were combined in an analysis of variance and the results are presented in Table 16. Survival was not the same in both years as indicated by the significant years main

Table 14. Analyses of variance for survival of European corn borer larvae in the laboratory on ten inbred lines in 1960 and 1961

Source of variation	Degrees of freedom	Mean square	F value
	1960[a]		
Replications	2	459.30	10.058**
Lines	9	710.06	15.549**
Error a	18	45.67	
Dates	8	3826.14	31.293**
Linear Regression	1	6676.84	54.608**
Quadratic Regression	1	60.74	.497
Deviations	6	3978.59	32.540**
Error b	16	122.27	
Lines x Dates	72	67.83	1.169
Error c	144	58.03	
	1961[b]		
Replications	2	485.88	7.151**
Lines	9	470.55	6.925**
Error a	18	67.95	
Dates	6	3422.98	13.942**
Linear Regression	1	17361.54	70.713**
Quadratic Regression	1	400.31	1.630
Deviations	4	694.01	2.827
Error b	12	245.52	
Lines x Dates	54	88.25	1.344
Error c	108	65.68	

[a]Coefficient of variation was 27.07 percent.

[b]Coefficient of variation was 24.25 percent.

**Significant differences at the 1 percent level of probability.

effect. The years x lines interaction was significant at the five percent level of probability. This indicated that relative positions of lines were somewhat variable for the two years.

Average growth of five day old larvae on all ten lines as measured by

Table 15. Ranked arcsin transformed means for survival of European corn borer larvae in the laboratory on ten inbred lines with Duncan's New Multiple Range Test applied[a]

1960

W22	CI31A	B14	K150	Oh45	L317	B42	M14	B37	WF9
21.12	22.31	26.11	26.34	26.55	27.20	27.82	32.81	33.22	37.88

1961

L317	CI31A	W22	B42	Oh45	K150	B37	M14	B14	WF9
26.73	27.24	29.26	31.25	33.48	35.38	35.66	36.87	37.27	41.24

[a]Any two means which are underscored by the same line are not significantly different at the 1 percent level of probability.

Table 16. Combined analysis of variance for survival of European corn borer larvae in the laboratory on ten inbred lines in 1960 and 1961[a]

Source of variation	Degrees of freedom	Mean square	F value
Years	1	421.83	57.052**
Replications within Years	4	60.29	8.154**
Lines	9	127.92	7.019**
Years x Lines	9	18.22	2.465*
Replications within Years x Lines	36	7.39	

[a]Coefficient of variation was 8.83 percent.

*Significant differences at the 5 percent level of probability.

**Significant differences at the 1 percent level of probability.

percent of second instar larvae of those which survived tended to be somewhat curvilinear across dates with an increasing rate up to a point then leveling off at about 60 percent (Figures 10 and 11). The average leveling off point for the five high lines (WF9, B14, M14, B37, and K150) was about 75 percent and for the five low lines (L317, W22, Oh45, B42, and CI31A) about 40 percent. This indicated that growth of larvae tended to increase as plants became older up to a point, then regardless of the number which survived only a given percent could reach the second instar in five days of feeding under the conditions of these experiments.

Investigations of Six Single Crosses

Field infestations

Survival of larvae   Differences were observed in survival levels of European corn borer larvae among the six single crosses when tested in the field in 1961. These differences were significant at the one percent level of probability as indicated by the analysis of variance (Table 17). Single cross means from the transformed data were ranked and Duncan's New Multiple Range Test (Duncan 1955) was used to compare each mean with every other mean. Results of the Duncan's test at the one percent level of probability are presented in Table 18.

The numbers of larvae which survived as calculated by retransforming the square root transformed means were correlated with average corn borer leaf-feeding ratings. This correlation ($r = 0.976$) was significant at the one percent level of probability.

The analysis of variance indicated that survival levels for the dates of infestation were significantly different. The breakdown of dates into linear, quadratic, and deviations from linear and quadratic components

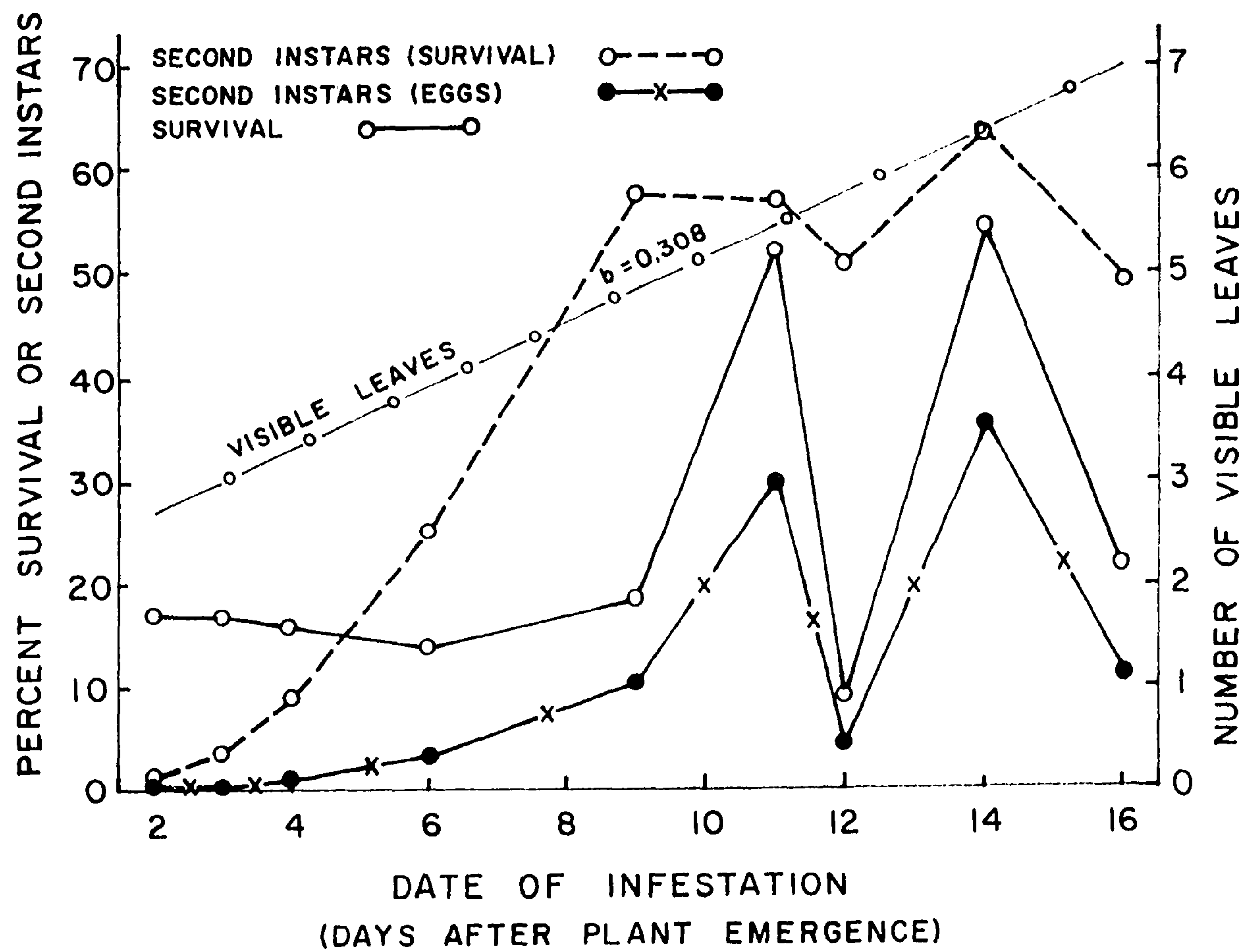

Figure 10. Average survival and growth patterns (growth measured as percentages of eggs applied or surviving larvae which reached the second instar) of young European corn borer larvae on whorl sections of ten inbred lines tested in the laboratory in 1960

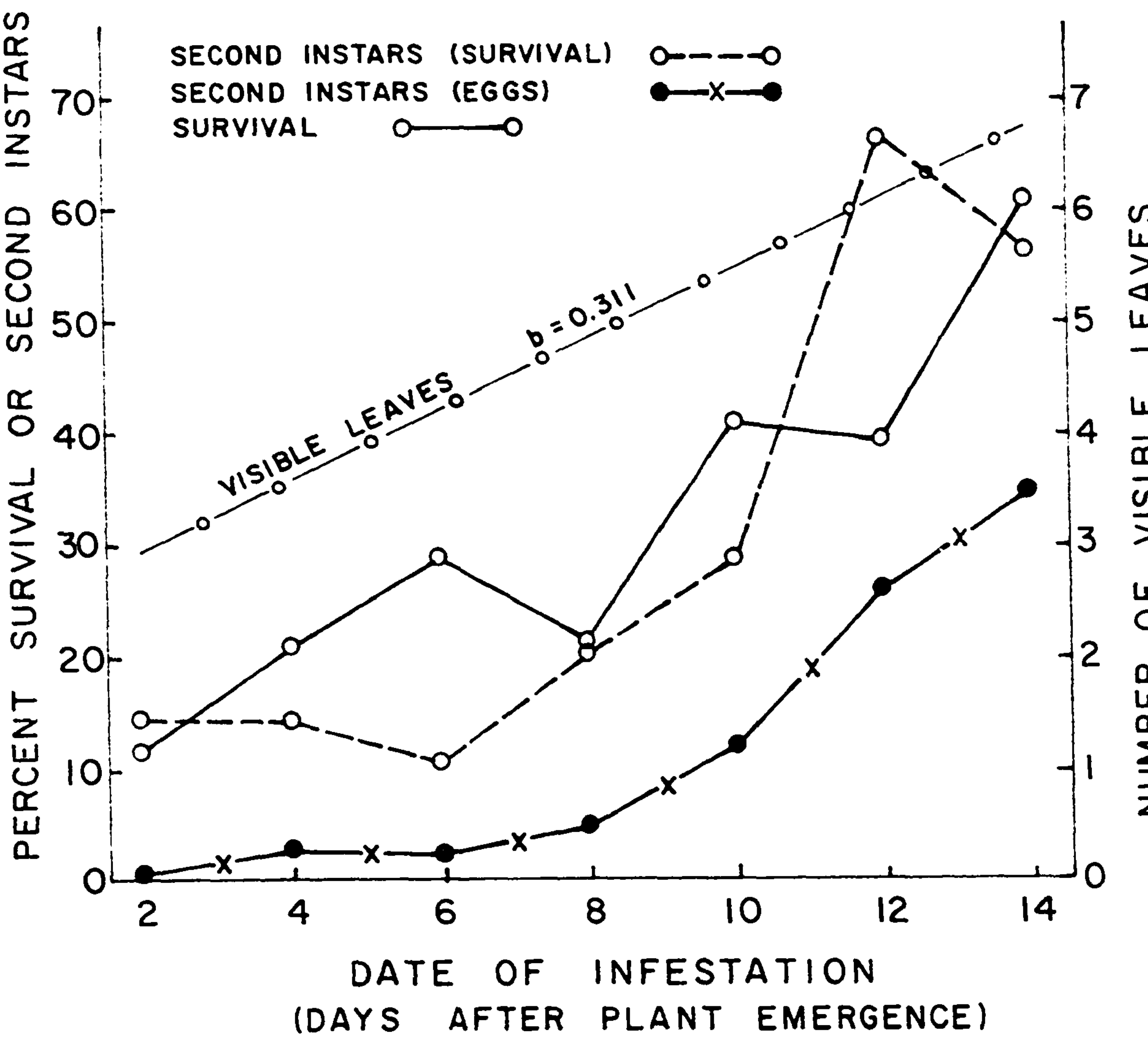

Figure 11. Average survival and growth patterns (growth measured as percentages of eggs applied or surviving larvae which reached the second instar) of young European corn borer larvae on whorl sections of ten inbred lines tested in the laboratory in 1961

Table 17. Analysis of variance for survival of European corn borer larvae in the field on six single crosses in 1961[a]

Source of variation	Degrees of freedom	Mean square	F value
Replications	3	.178	1.061
Single Crosses	5	2.156	12.858**
Error a	15	.168	
Dates	5	1.510	19.483**
Linear Regression	1	7.166	92.462**
Quadratic Regression	1	.006	.000
Deviations	3	.126	1.615
Error b	15	.078	
Single Crosses x Dates	25	.094	1.394
Error c	75	.067	

[a]Coefficient of variation was 16.37 percent.

**Significant at the 1 percent level of probability.

Table 18. Ranked square root transformed means for survival of European corn borer larvae in the field on six single crosses in 1961 with Duncan's New Multiple Range Test applied[a]

B42 x W22	CI31A x Oh45	CI31A x WF9	B42 x WF9	M14 x WF9	B37 x WF9
1.27	1.34	1.44	1.55	1.90	1.99

[a]Any two means which are underscored by the same line are not significantly different at the 1 percent level of probability.

indicated that most of the variation in survival for the dates of infestation was due to the linear component. Average survival of larvae for ten lines on six dates of infestation are presented in Figure 12. Averages of the susceptible x susceptible, resistant x susceptible, and resistant x resistant single crosses also are presented in this figure. These data indicated that larvae were better able to survive on older plants. The rates of increased survival were not the same for all single crosses. The increase in rate of survival on susceptible x susceptible single crosses was more rapid than on resistant x susceptible or resistant x resistant single crosses and increase on resistant x susceptible single crosses was slightly more rapid than on resistant x resistant single crosses. In other words, single crosses tended to have wider differences in survival of young larvae on older plants. Although this tendency was observed, the mean square for the single crosses x dates interaction which tested these differences was not significant at the five percent level of probability.

Average numbers of visible leaves of single cross plants infested on the various dates are presented in Figure 12 as a linear regression line. Single cross plants added about 0.37 visible leaves per day up to 14 days after plant emergence.

<u>Location of larvae</u> When total survival of larvae on single cross plants infested in the field was examined on the basis of where larvae were located, it was evident that survival rates were different among single crosses for the three areas of young plants. Average survival data in numbers and percentages of larvae are presented in Table 19 for the low, whorl, and exposed leaf areas of the six single crosses. Average numbers

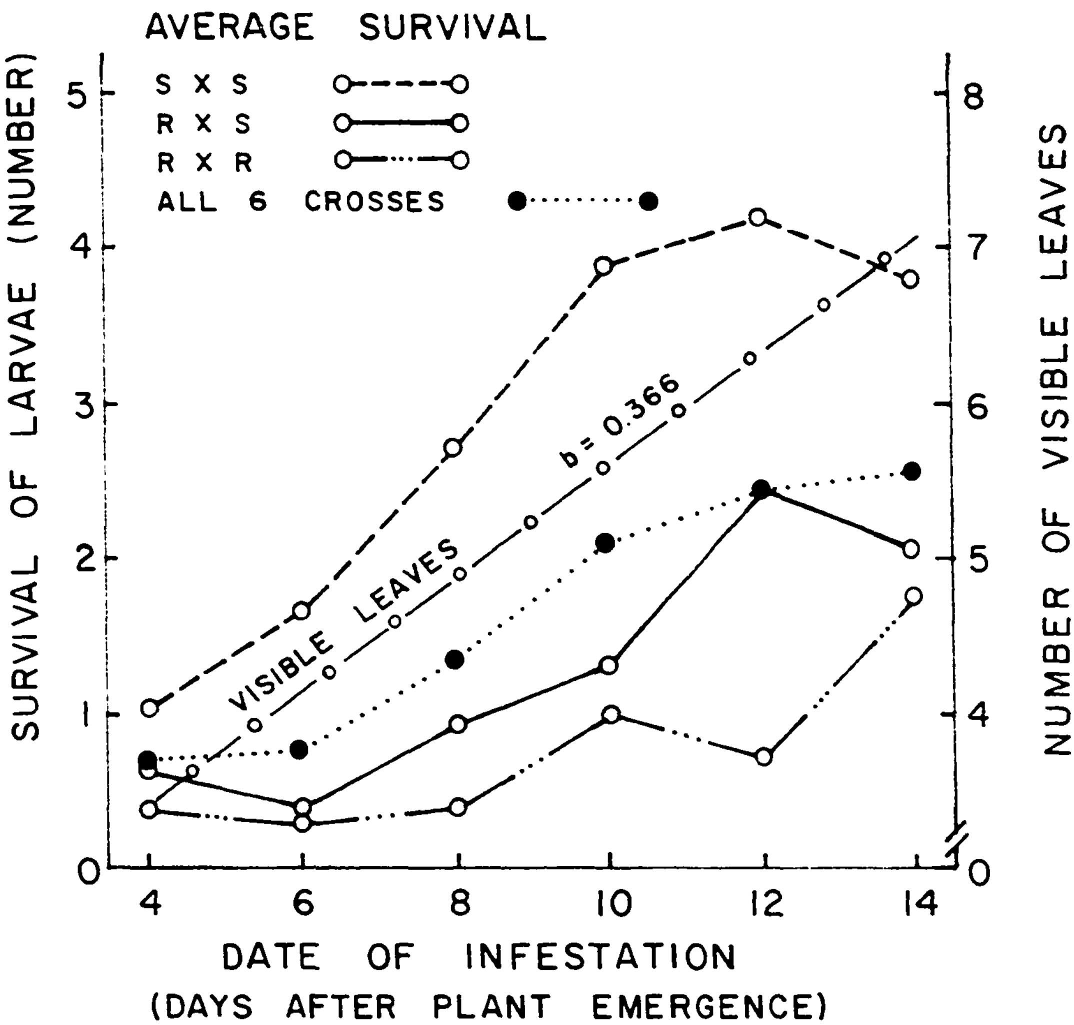

Figure 12. Average survival patterns of European corn borer larvae after 5 days of feeding on young plants of six single crosses infested in the field in 1961

Table 19. Average survival in numbers and percentages of European corn borer larvae for three plant areas of six single crosses in 1961

Single cross	Plant area: Low Number	Low Percent	Whorl Number	Whorl Percent	Exposed Leaf Number	Exposed Leaf Percent	Total survival
			Susceptible x Susceptible				
B37 x WF9	.64	19.95	2.43	75.20	.16	4.85	3.23
M14 x WF9	.65	23.36	1.94	69.47	.20	7.17	2.79
Average	.65		2.19		.18		3.02
			Susceptible x Resistant				
B42 x WF9	.67	43.93	.75	49.71	.10	6.36	1.52
CI31A x WF9	.39	33.59	.67	58.01	.10	8.40	1.16
Average	.52		.71		.10		1.33
			Resistant x Resistant				
B42 x W22	.26	42.86	.29	47.14	.06	10.00	.61
CI31A x Oh45	.20	22.33	.55	61.17	.15	16.50	.90
Average	.23		.42		.11		.76

of larvae in each area also are presented for the susceptible x susceptible, resistant x susceptible, and resistant x resistant groups of single crosses. Differences in numbers of larvae which survived in the three plant areas of six single crosses were transformed using the square root transformation and tested by analyses of variance (Table 20). The total analysis indicated that survival was different on the single crosses and also in the three plant areas. These differences were significant at the

Table 20. Analyses of variance for survival of European corn borer larvae in three plant areas of six single crosses in 1961

Source of variation	Degrees of freedom	Mean square	F value
Total for all three areas[a]			
Replications	3	.605	.593
Single crosses	5	12.087	11.838**
Error a	15	1.021	
Areas	2	63.847	158.982**
Single Crosses x Areas	10	4.152	10.338**
Error b	36	.402	
Low area[b]			
Replications	3	.155	.463
Single Crosses	5	2.776	8.319**
Among groups	2	6.064	18.173**
R x R vs S x S	1	11.340	33.983**
R x S vs 1/2 (R x R+ S x S)	1	.788	2.361
Within groups	3	.584	1.751
Error	15	.334	
Whorl area[c]			
Replications	3	.721	.629
Single Crosses	5	17.036	14.857**
Among groups	2	40.702	35.498**
R x R vs S x S	1	75.169	65.558**
R x S vs 1/2 (R x R + S x S)	1	6.169	5.380*
Within groups	3	1.258	1.097
Error	15	1.147	
Exposed leaf area[d]			
Replications	3	.325	.842
Single Crosses	5	.486	1.259
Among groups	2	.706	1.829
R x R vs S x S	1	.888	2.303
R x S vs 1/2 (R x R + S x S)	1	.523	1.355
Within groups	3	.339	.879
Error	15	.386	

[a]Coefficient of variation was 5.43 percent.

[b]Coefficient of variation was 15.67 percent.

[c]Coefficient of variation was 20.12 percent.

[d]Coefficient of variation was 30.15 percent.

*Significant differences at the 5 percent level.

**Significant differences at the 1 percent level.

one percent level of probability. The total analysis also indicated that single crosses did not give the same rates of survival in each area, since the single crosses x areas interaction was significant at the one percent level.

Each plant area was analysed separately to determine whether or not survival among single crosses was different in each area. These analyses indicated that single crosses were significantly different at the one percent level for the low and whorl areas, but were not different for the exposed leaf area. The variations among single crosses in each area were broken down into two components, among groups and within groups. The among groups component was further broken down into two comparisons as follows: comparison of resistant x resistant versus susceptible x susceptible single crosses and comparison of resistant x susceptible versus the mean of resistant x resistant plus susceptible x susceptible single crosses. This second comparison measures the tendency for dominant effects of resistance or susceptibility. Most of the single cross variation was due to the among groups component in the low and whorl areas. Resistant x resistant single crosses were significantly different at the one percent level from the susceptible x susceptible single crosses in both low and whorl areas. Survival of larvae in the whorl area of resistant x susceptible single crosses was significantly different at the five percent level from the mean of resistant x resistant plus susceptible x susceptible single crosses. These differences indicated that resistance to feeding in the whorl area tends to be dominant. Mean survival of larvae in the low, whorl, and exposed leaf areas for each group of single crosses is presented in Figure 13.

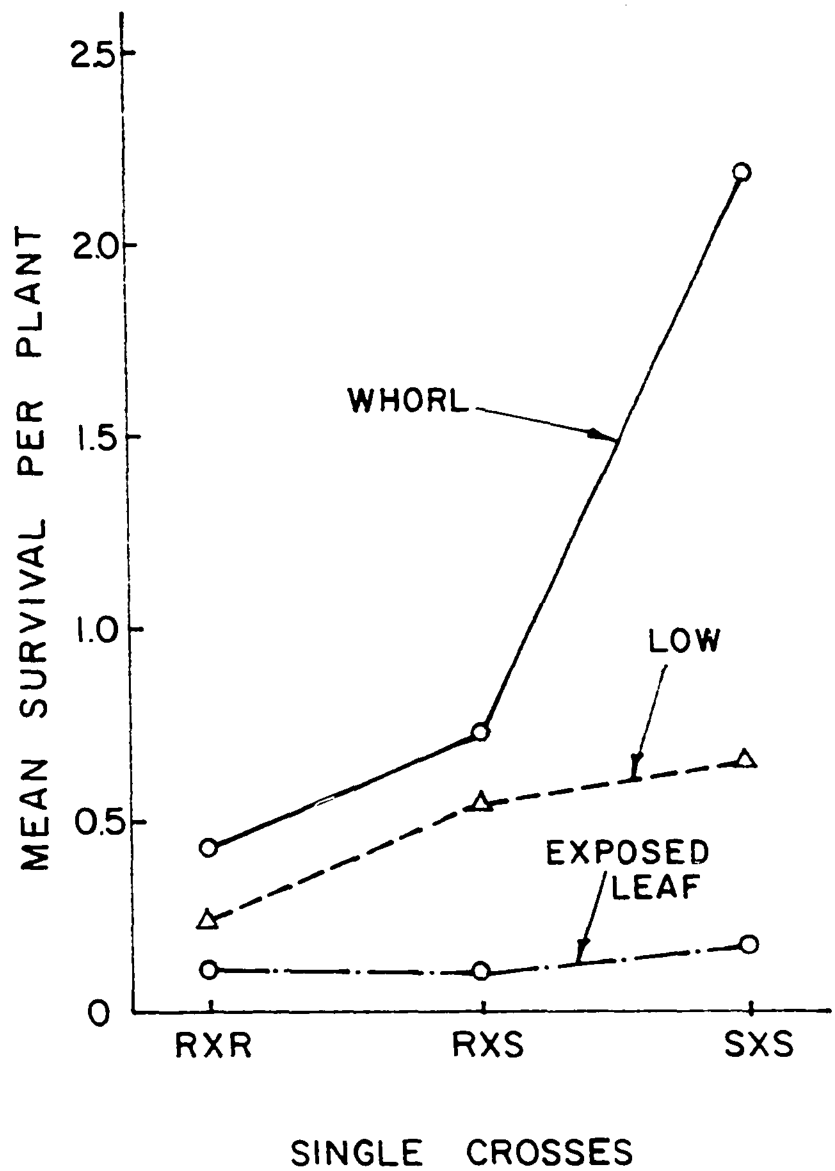

Figure 13. Average survival patterns of young European corn borer larvae in three plant areas of resistant x resistant, resistant x susceptible, and susceptible x susceptible single crosses in 1961

Laboratory infestations

Average survival percentages and growth rates in terms of second instar larvae are presented in Table 21 for six single crosses tested in the laboratory under controlled temperature and humidity conditions. Two values are presented for percent of second instar larvae, one was calculated on the basis of total survival and the other on the basis of total eggs applied to each single cross. Variations in survival among single crosses were not significant as indicated by the analysis of variance on the arcsin transformed data presented in Table 22.

The average survival and growth data, presented in Table 21, were each correlated with the average corn borer leaf-feeding ratings. In addition to these simple correlations a multiple correlation was calculated for percent survival and percent of second instar larvae of those which survived with the average corn borer leaf-feeding ratings. Simple and multiple correlation coefficients are presented at the bottom of Table 22. Correlation of survival on average leaf-feeding ratings was significant at the five percent level of probability. All other correlations were significant at the one percent level of probability. Measures of larval growth tended to give higher correlations than survival for the six single crosses.

The age of single cross plants at the time of infestation influenced the rate of survival in the laboratory studies. Larger percentages of larvae survived on older plants than on younger plants. The analysis of variance indicated that differences in survival among dates of infestation were significant at the one percent level. The breakdown of dates into linear, quadratic, and deviations from linear and quadratic components

Table 21. Average survival and growth of European corn borer larvae in the whorl areas of six single crosses tested in the laboratory in 1961 with simple and multiple correlation coefficients (r and R values)

Single cross	Average corn borer rating	Percent survival	Percent second instar[a]	Percent second instar[b]
B37 x WF9	8.0	38.55	63.21	24.36
M14 x WF9	8.0	34.72	50.33	17.48
B42 x WF9	4.5	39.66	48.16	19.10
CI31A x WF9	3.5	32.45	35.19	11.42
B42 x W22	3.0	32.85	25.55	8.39
CI31A x Oh45	2.0	28.96	25.31	7.33
Average		34.53	41.29	14.68
Simple r value[c]		.641*	.909**	.863**
Multiple R value[d]		----	.932**	----

[a]Percent of second instar larvae of those which survived.

[b]Percent of second instar larvae of the total eggs applied.

[c]Simple correlation of survival or larval growth with average corn borer leaf-feeding ratings.

[d]Multiple correlation of percent survival plus percent of second instar larvae of those which survived with average corn borer leaf-feeding ratings.

*Correlation significant at the 5 percent level of probability.

**Correlation significant at the 1 percent level of probability.

Table 22. Analysis of variance for survival of European corn borer larvae in the laboratory on six single crosses in 1961[a]

Source of variation	Degrees of freedom	Mean square	F value
Replications	2	553.83	4.713
Single Crosses	5	124.23	1.057
Error a	10	117.51	
Dates	6	3993.42	59.657**
Linear Regression	1	17349.14	259.174**
Quadratic Regression	1	2462.64	36.789**
Deviations	4	1037.18	15.494**
Error b	12	66.94	
Single Crosses x Dates	30	61.92	.962
Error c	60	64.40	

[a]Coefficient of variation was 22.37 percent.

**Significant differences at the 1 percent level of probability.

revealed that most of the variation was due to the linear component; however, quadratic and deviations from linear and quadratic components were both significant at the one percent level.

The mean square for the single crosses x dates interaction was not significant in the analysis of variance which indicated that single crosses tended to maintain their relative positions on the dates of infestation.

Average percent survival and percentages of second instar larvae are presented in Figure 14 for each date of infestation. The number of visible leaves is also presented in this figure as a linear regression line. An average of 0.36 visible leaves were added to each single cross plant for each day of growth up to 14 days after plant emergence. More second instar larvae were observed in the laboratory after five days of

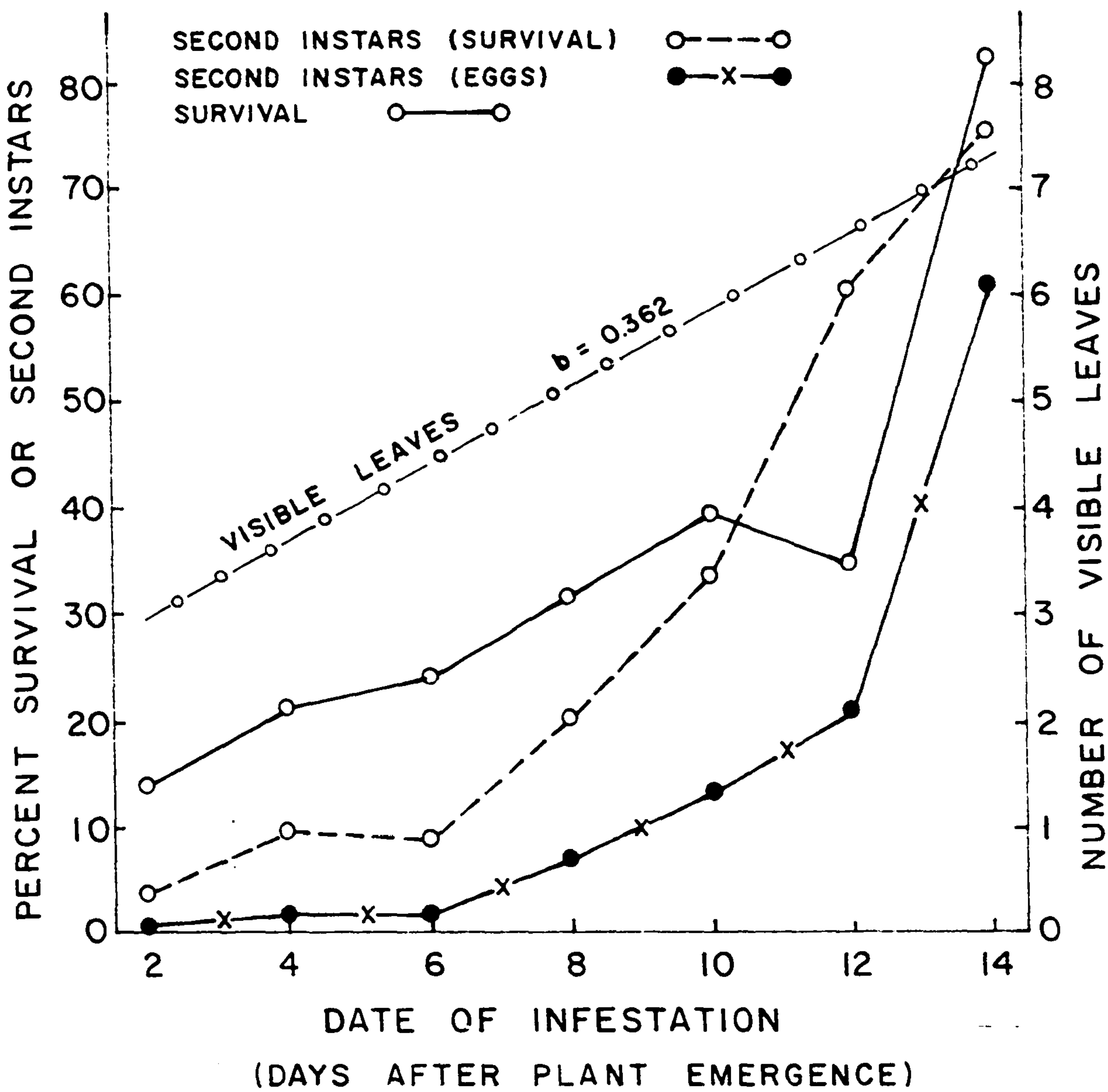

Figure 14. Average survival and growth patterns (growth measured as percentages of eggs applied or surviving larvae which reached the second instar) of young European corn borer larvae on whorl sections of six single crosses tested in the laboratory in 1961

feeding on single cross plants infested on the later dates.

Investigations of Six Related Inbred Lines

Field infestations

Survival of larvae   Differences were observed in the number of larvae which survived on the six related inbred lines when tested in the field. The analysis of variance (Table 23) indicated that these differences were significant at the one percent level of probability. Square root transformed means were ranked and Duncan's New Multiple Range Test (Duncan 1955) was applied (Table 24).

Table 23. Analysis of variance for survival of European corn borer larvae in the field on six related inbred lines in 1961[a]

Source of variation	Degrees of freedom	Mean square	F value
Replications	1	.187	4.675
Lines	5	1.120	28.000**
Error a	5	.040	
Ears within Lines	6	.031	.113
Error b	6	.275	
Dates	5	2.478	85.148**
Linear Regression	1	11.522	396.976**
Quadratic Regression	1	.465	15.962*
Deviations	3	.124	4.276
Error c	5	.029	
Lines x Dates	25	.087	2.674**
Error d	25	.033	
Ears within Lines x Dates	30	.107	3.156**
Error e	30	.034	

[a]Coefficient of variation was 11.65 percent.

*Significant at the 5 percent level of probability.

**Significant at the 1 percent level of probability.

Table 24. Ranked square root transformed means for survival of European corn borer larvae in the field on six related inbred lines with Duncan's New Multiple Range Test applied[a]

1405	1426	1406	1400	1412	WF9
1.23	1.48	1.57	1.65	1.70	1.87
			———	———	———
	———	———	———	———	
———					

[a]Any two means which are underscored by the same line are not significantly different at the 1 percent level of probability.

The transformed means were retransformed and these were correlated with the three year average corn borer leaf-feeding ratings. This correlation was significant at the one percent level. The correlation coefficient was 0.828.

Survival of larvae was not different for the two seed sources of each line as indicated in the analysis of variance by the significant mean square for ears within lines. However, survival of larvae on plants from the two sources of seed varied significantly at the one percent level for dates of infestation as indicated in the analysis of variance by the ears within lines x dates interaction.

Main effects for dates of infestation were highly significant at the one percent level. Linear and quadratic components accounted for most of the variation among dates. Average survival of larvae for each date of infestation is presented in Figure 15. These data indicated that older plants sustained larger numbers of larvae. Plant growth as measured by the number of visible leaves on the dates of infestation also are presented in Figure 15 as a linear regression line. Plants of the six

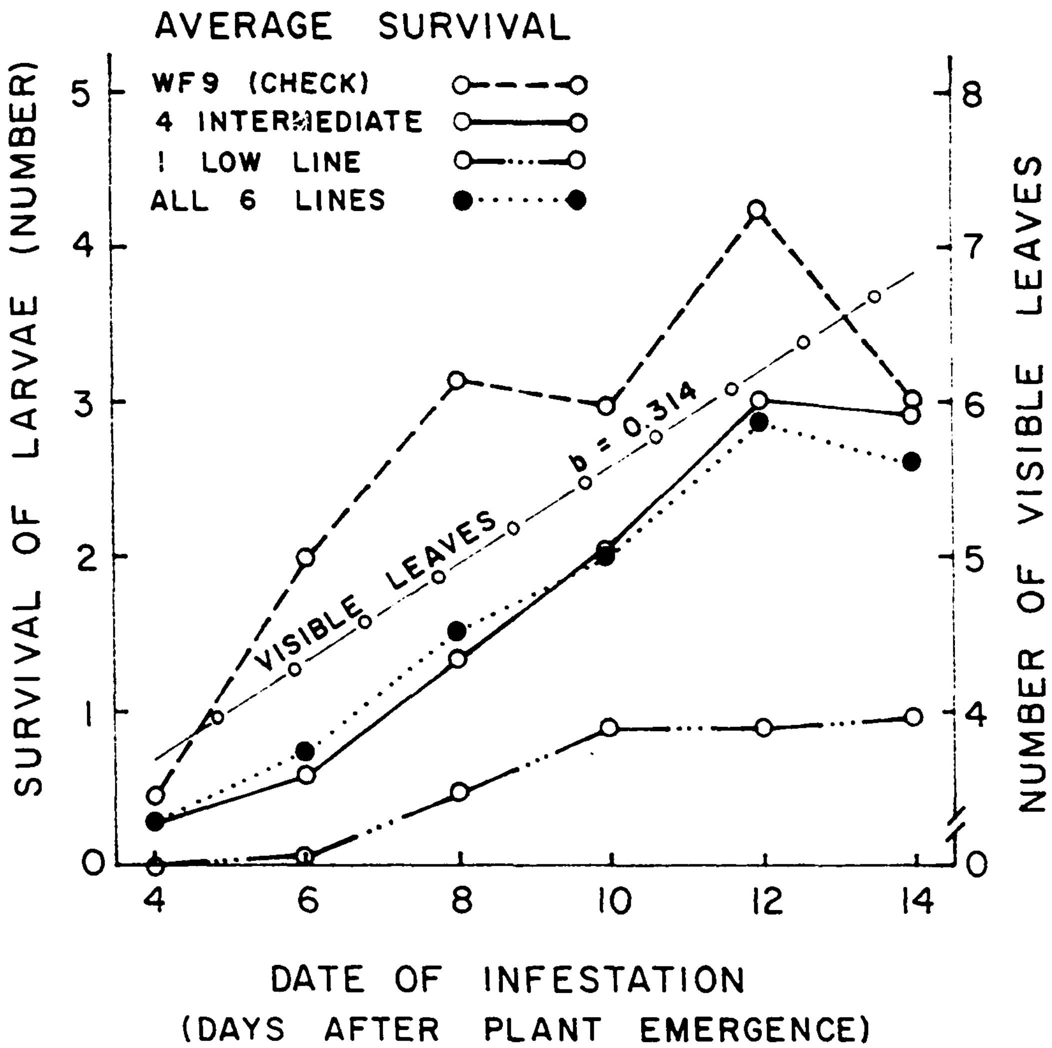

Figure 15. Average survival patterns of young European corn borer larvae after five days of feeding on young corn plants of six related inbred lines infested in the field in 1961

related inbreds added about 0.31 visible leaves per day up to 14 days after plant emergence.

The six related lines were arranged into three groups on the basis of larval survival, a single high line (WF9), four intermediate lines (1412, 1400, 1406, and 1426), and a single low line (1405). Average survivals for groups of lines are presented in Figure 15 for dates of infestation. Increases in the rates of survival were not the same for all groups. Line WF9 increased more rapidly than either of the other two groups and the intermidiate group increased more rapidly than the low line, 1405. These differences in rates of increased survival probably account for most of the variation observed in the lines x dates interaction. This interaction was significant at the one percent level of probability.

Distribution of larvae Average numbers and percentages of corn borer larvae which survived for five days in the low, whorl, and exposed leaf areas of six related lines are presented in Table 25. Analyses of variance were performed on square root transformed data and the results are presented in Table 26. Mean squares for lines, plant areas, and lines x areas were all significant in the total analysis, so survival on lines was analysed separately for each area. Significant differences were observed at the one percent level in the low and whorl areas. Variations in survival of larvae on the exposed leaf area were not significant. The significant lines x areas interaction indicated that the relative positions of survival levels on lines were different in the three plant areas.

Table 25. Average survival, numbers and percentages, of European corn borer larvae in three plant areas of six related inbred lines in 1961

Inbred line	Plant area: Low Number	Low Percent	Whorl Number	Whorl Percent	Exposed Leaf Number	Exposed Leaf Percent	Total survival
WF9	.89	30.96	1.81	62.99	.17	6.05	2.87
1406	.66	37.79	.93	52.91	.16	9.30	1.75
1412	1.01	46.26	1.01	46.26	.16	7.48	2.18
1400	.68	32.81	1.20	58.19	.19	9.10	2.07
1426	.40	28.47	.94	67.15	.06	4.38	1.40
1405	.29	44.44	.29	44.44	.07	11.12	.65
Average	.65		1.03		.14		1.82

Laboratory infestation

Survival of larvae on the six related lines ranged from 24.89 percent on 1426 to 45.36 percent on WF9 when tested in the laboratory under controlled conditions. Average percent survival and percentages of second instar larvae are presented in Table 27 for each line. Larval growth is presented for each line in two ways: percent of all surviving larvae which reached the second instar and percent of total eggs applied which reached the second instar. Percent survival and percentages of second instar larvae were each correlated with average corn borer leaf-feeding ratings. In addition to these simple correlations a multiple correlation was made for percent survival and percent of second instar larvae of those

Table 26. Analyses of variance for survival of European corn borer larvae in three plant areas of six related inbred lines in 1961

Source of variation	Degrees of freedom	Mean square	F value
	Total for all three areas[a]		
Replications	3	.587	.929
Lines	5	6.555	10.376**
Error a	15	.632	
Areas	2	54.506	202.025**
Lines x Areas	10	1.475	5.466**
Error b	36	.270	
	Low area[b]		
Replications	3	.421	1.491
Lines	5	2.899	10.270**
Error	15	.282	
	Whorl area[c]		
Replications	3	.323	.580
Lines	5	6.142	11.027**
Error	15	.557	
	Exposed leaf area[d]		
Replications	3	.068	.173
Lines	5	.464	1.174
Error	15	.395	

[a]Coefficient of variation was 14.22 percent.

[b]Coefficient of variation was 13.23 percent.

[c]Coefficient of variation was 15.10 percent.

[d]Coefficient of variation was 31.50 percent.

**Significant at the 1 percent level of probability.

Table 27. Average survival and growth of European corn borer larvae in the whorl areas of six related inbred lines tested in the laboratory in 1961 with simple and multiple correlation coefficients (r and R values)

Inbred line	Average corn borer rating	Percent survival	Percent second instar[a]	Percent second instar[b]
WF9	8.50	45.36	46.79	21.22
1406	5.67	34.61	36.58	12.66
1412	4.25	32.22	20.81	6.70
1400	3.50	28.36	28.06	7.96
1426	3.17	24.89	17.39	4.32
1405	2.25	27.92	23.75	6.63
Average		32.23	28.89	9.92
Simple r value[c]		.961**	.893**	.949**
Multiple R value[d]		----	.962**	----

[a]Percent of second instar larvae of those which survived.

[b]Percent of second instar larvae of the total eggs applied.

[c]Simple correlation of survival or larval growth with average corn borer leaf-feeding ratings.

[d]Multiple correlation of percent survival plus percent of second instar larvae of those which survived with average corn borer leaf-feeding ratings.

**Correlation significant at the 1 percent level of probability.

which survived with the average corn borer leaf-feeding ratings. These correlations were all significant at the one percent level as indicated by the correlation coefficients presented at the bottom of Table 27.

The analysis of variance of arcsin transformed data indicated that variations among the six related lines were not significant (Table 28). However, as suggested by Steel and Torrie (1960) the Duncan's New Multiple Range Test was applied to the transformed means and significant differences were observed at the five percent level of probability (Table 29). Steel and Torrie indicated that Duncan's test can be used regardless of whether or not the F value was significant. As indicated by Cochran and

Table 28. Analysis of variance for survival of European corn borer larvae in the laboratory on six related inbred lines in 1961[a]

Source of variation	Degrees of freedom	Mean square	F value
Replications	1	157.59	.607
Lines	5	571.30	2.201
Error a	5	259.55	
Ears within Lines	6	41.66	.343
Error b	6	121.49	
Dates	6	2342.95	14.301**
Linear Regression	1	13262.73	80.954**
Quadratic Regression	1	.39	.002
Deviations	4	198.64	1.212
Error c	6	163.83	
Lines x Dates	30	96.63	1.728
Error d	30	55.92	
Ears within Lines x Dates	36	51.34	1.975*
Error e	36	26.00	

[a]Coefficient of variation was 15.25 percent.

*Significant at the 5 percent level of probability.

**Significant at the 1 percent level of probability.

Table 29. Ranked arcsin transformed means for survival of European corn borer larvae in the laboratory for six related inbred lines with Duncan's New Multiple Range Test applied[a]

1426	1400	1405	1412	1406	WF9
28.42	30.96	31.17	34.04	34.65	41.42

[a]Any two means which are underscored by the same line are not significantly different at the 5 percent level of probability.

Cox (1957) the Duncan's test is more sensitive because the level of protection against erroneously finding significant differences is decreased as more means are added for comparison.

The analysis of variance indicated that survival of larvae on plants of the two seed sources was not significantly different; however, the mean square for ears within lines x dates interaction was significant at the five percent level. This indicated that survival was quite variable between seed sources for the dates of infestation.

Survival of corn borer larvae was different on the dates of infestation. The analysis of variance indicated that these differences were significant at the one percent level, and further that most of the variation was due to the linear component. Progressively more larvae could survive on plants as they became older and larger as illustrated in Figure 16. Not only were more larvae able to survive on older plants, but also these larvae were able to grow more rapidly. This was indicated by the average percentages of second instar larvae on dates of infestation (Figure 16). Average plant growth, measured by the number of visible

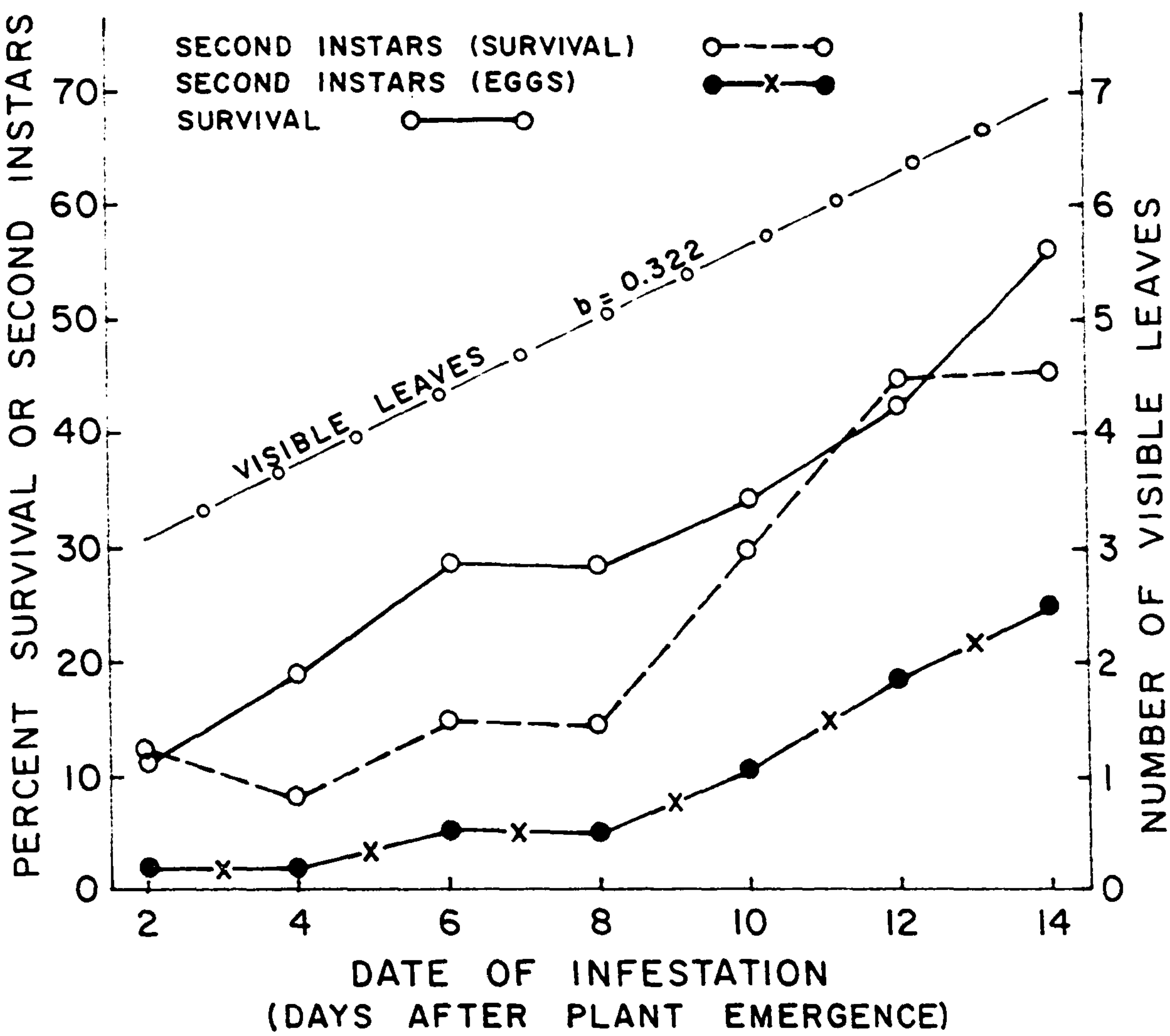

Figure 16. Average survival and growth patterns (growth measured as percentages of eggs applied or surviving larvae which reached the second instar) of young European corn borer larvae on whorl sections of six related inbred lines tested in the laboratory in 1961

leaves is also presented in this figure as a linear regression line. Plants of the six related inbred lines added about 0.32 visible leaves for each day of growth up to 14 days after plant emergence.

Arrangement of Leaf Structures

Wide differences were observed among the ten inbred lines and six single crosses for measurements of the following leaf characteristics: area per bulliform hair, distance between bulliform hairs along bulliform groups, and distance between bulliform groups across leaf samples. These differences were tested by analyses of variance (Tables 30 and 31) and were observed to be significant. Measurements of these same leaf characteristics among the six related inbreds were not significantly different.

The means were ranked for these leaf characteristics and Duncan's New Multiple Range Test (Duncan 1955) was applied. These are illustrated in Tables 32 and 33 for the ten inbred lines and six single crosses. These ranked means were correlated with average corn borer leaf-feeding ratings and the correlation coefficients are presented at the bottom of these tables. Only one significant correlation was observed. This was the correlation of the distance between bulliform groups across the leaf samples for the six single crosses. Shapes of the leaf pieces in each sample, used as a form of replication, were not important except in measurements of the distance between bulliform groups across leaf samples for the six single crosses. The wide pieces tended to give larger and probably more accurate values than the narrow pieces in this measurement.

Widths of bulliform groups were quite variable among the ten inbred lines and six single crosses, but only small variations were observed

Table 30. Analyses of variance for various arrangements of bulliform structures on mature corn leaves of ten inbred lines

Source of variation	Degrees of freedom	Mean square	F value
		Area of leaf per bulliform hair[a]	
Lines	9	.7637	46.285**
Shapes	1	.0045	.273
Lines x Shapes	9	.0165	
		Distance between bulliform hairs[b]	
Lines	9	.8795	146.583**
Shapes	1	.0001	.017
Lines x Shapes	9	.0060	
		Distance between bulliform groups[c]	
Lines	9	.0401	8.907**
Shapes	1	.0082	1.818
Lines x Shapes	9	.0045	

[a]Coefficient of variation was 8.52 percent.

[b]Coefficient of variation was 4.84 percent.

[c]Coefficient of variation was 7.58 percent.

**Significant differences at the 1 percent level of probability.

among the six related inbred lines. The analyses of variance (Table 34) indicated that the differences in widths of bulliform groups were significant at the one percent level among the ten inbreds and six single crosses, but were not significant among the six related inbreds.

Mean widths of bulliform groups, measured in microns, were ranked and the Duncan's New Multiple Range Test (Duncan 1955) was applied to the ten inbred lines (Table 35) and six single crosses (Table 36). These ranked means were correlated with average corn borer leaf-feeding ratings and the

Table 31. Analyses of variance for various arrangements of bulliform structures on mature corn leaves of six single crosses

Source of variation	Degrees of freedom	Mean square	F value
	Area of leaf per bulliform hair[a]		
Single Crosses	5	1.3810	36.057**
Shapes	1	.0646	1.687
Single Crosses x Shapes	5	.0383	
	Distance between bulliform hairs[b]		
Single Crosses	5	1.4529	25.093**
Shapes	1	.0146	.252
Single Crosses x Shapes	5	.0579	
	Distance between bulliform groups[c]		
Single Crosses	5	.0083	6.932*
Shapes	1	.0138	11.488*
Single Crosses x Shapes	5	.0012	

[a]Coefficient of variation was 9.58 percent.

[b]Coefficient of variation was 11.55 percent.

[c]Coefficient of variation was 11.35 percent.

*Significant differences at the 5 percent level of probability.

**Significant differences at the 1 percent level of probability.

correlation coefficients are presented at the bottom of Tables 35 and 36. Neither of these correlations were significant which indicated that widths of the bulliform groups of these samples were not related to corn borer resistance.

Table 32. Ranked means for various arrangements of bulliform structures on mature corn leaves of ten inbred lines with Duncan's New Multiple Range Test applied[a]

Area of leaf per bulliform hair[b] ($\sqrt{\text{sq mm}}$)

B14	B37	CI31A	K150	M14	L317	W22	Oh45	WF9	B42
.93	1.03	1.07	1.20	1.23	1.40	1.63	1.67	1.94	3.01

Distance between bulliform hairs[c] ($\sqrt{\text{mm}}$)

B37	B14	CI31A	K150	M14	W22	L317	Oh45	WF9	B42
1.08	1.10	1.17	1.31	1.39	1.44	1.58	1.67	1.69	3.32

Distance between bulliform groups[d] (mm)

B14	M14	L317	CI31A	B42	K150	B37	WF9	Oh45	W22
.725	.777	.781	.819	.821	.844	.907	.979	.995	1.202

[a]Any two means which are underscored by the same line are not significantly different at the 1 percent level.

[b]Correlation coefficient with corn borer leaf-feeding ratings was 0.37.

[c]Correlation coefficient with corn borer leaf-feeding ratings was -0.37.

[d]Correlation coefficient with corn borer leaf-feeding ratings was -0.07.

Table 33. Ranked means for various arrangements of bulliform structures on mature corn leaves of six single crosses with Duncan's New Multiple Range Test applied[a]

Area of leaf per bulliform hair[b] ($\sqrt{\text{sq mm}}$)

CI31A x WF9	B42 x WF9	CI31A x Oh45	M14 x WF9	B37 x WF9	B42 x W22
1.30	1.43	1.58	1.85	2.70	3.40

Distance between bulliform hairs[c] ($\sqrt{\text{mm}}$)

CI31A x WF9	B42 x WF9	CI31A x Oh45	M14 x WF9	B37 x WF9	B42 x W22
1.33	1.52	1.66	1.79	2.69	3.53

Distance between bulliform groups[d] (mm)

B42 x WF9	CI31A x Oh45	B42 x W22	CI31A x WF9	B37 x WF9	M14 x WF9
.906	.913	.933	.951	1.016	1.069

[a]Any two means which are underscored by the same line are not significantly different at the 1 percent level.

[b]Correlation coefficient with average corn borer leaf-feeding ratings was 0.14.

[c]Correlation coefficient with average corn borer leaf-feeding ratings was 0.08.

[d]Correlation coefficient with average corn borer leaf-feeding ratings was 0.88.

Table 34. Analyses of variance for widths of bulliform groups on ten inbred lines, six single crosses, and six related inbred lines

Source of variation	Degrees of freedom	Mean square	F value
Ten inbred lines[a]			
Lines	9	15.91	4.483**
Pieces within Lines	40	3.55	
Six single crosses[b]			
Single Crosses	5	18.57	4.850**
Pieces within Single Crosses	24	3.83	
Six related inbred lines[c]			
Lines	5	4.74	1.258
Sources within Lines	6	3.77	.887
Pieces within Sources	48	4.25	

[a]Coefficient of variation was 13.38 percent.

[b]Coefficient of variation was 13.91 percent.

[c]Coefficient of variation was 14.83 percent.

**Significant differences at the 1 percent level of probability.

Table 35. Ranked mean widths of bulliform groups[a] measured in microns for the ten inbred lines with Duncan's New Multiple Range Test applied[b]

CI31A	M14	W22	Oh45	WF9	B14	L317	B42	B37	K150
75	79	82	87	93	97	99	101	106	110

[a]Correlation coefficient with average corn borer leaf-feeding ratings was 0.22

[b]Any two means which are underscored by the same line are not significantly different at the 1 percent level of probability.

Table 36. Ranked mean widths of bulliform groups[a] measured in microns for the six single crosses with Duncan's New Multiple Range Test applied[b]

B42 x WF9	B37 x WF9	M14 x WF9	CI31A x Oh45	CI31A x WF9	B42 x W22
76	88	88	91	100	114

[a]Correlation coefficient with average corn borer leaf-feeding ratings was 0.19.

[b]Any two means which are underscored by the same line are not significantly different at the 1 percent level of probability.

DISCUSSION

Survival of European corn borer larvae was studied in field experiments on young corn plants of ten inbred lines in 1959, 1960, and 1961. Field experiments also were conducted on six single crosses and six related inbred lines in 1961. Significant differences in survival of larvae were observed among inbred lines and single crosses in each of these experiments. When average survival rates were plotted across the dates of infestation for experiment totals, the patterns observed were nearly linear as illustrated in Figures 7, 8, 9, 12, and 15. Levels of survival tended to increase at nearly a constant rate as older plants were infested. It appeared that older plants either became less resistant to feeding by the European corn borer larvae or they increased in their available leaf-feeding surfaces so that larger numbers of larvae could survive, or a combination of both.

Rates of increase in the survival levels were smaller on the more resistant entries than on the more susceptible entries. In other words, wider survival differences were observed on older plants, those infested on the later dates, than on younger plants, those infested on the earlier dates. The results obtained by earlier workers might be explained on the basis of the results observed in the present studies. These earlier workers reported that larvae were not able to survive in significant numbers on corn plants until the plants had reached heights of 16 to 18 inches. Since the present studies indicated that survival levels were generally low, and also that differences between resistant and susceptible plants were small on younger plants, the results obtained by earlier workers might have been expected. Another factor which might have contributed to the results reported in the earlier studies was that levels of corn borer resistance were not greatly different among the plant materials being tested by these workers.

Increased rates of corn borer survival were also observed in the laboratory experiments on these same plant materials (ten inbred lines, six single crosses, and six related inbred lines) as illustrated in Figures 10, 11, 14, and 16. The pattern of survival was somewhat variable for the ten inbred lines in 1960. Survival of larvae on some of the dates of infestation was low and inconsistant when compared with the levels obtained on other dates. Many of the plant samples were observed to decompose within the five day period of feeding. Survival levels were lower in those samples where plant decomposition was evident. Decomposition of the plant materials was probably due to the high moisture content of the plant samples when they were placed in the test tubes and infested. Methods of handling the plant samples were improved in the 1961 laboratory infestations in that plants were dried until the leaves had wilted before the whorl sections were removed and infested in the test tubes.

Growth rates of corn borer larvae were determined in the laboratory studies of the ten inbred lines in 1960 and 1961, and the six single crosses and six related inbred lines in 1961. Not only were the rates of survival improved when older plants were infested, but those larvae which survived were able to grow more rapidly as expressed by the larger percentages of second instar larvae observed on the later dates of infestation. It appears that older plants are better sources of food for corn borer larvae.

Survival of young corn borer larvae on young corn plants under field conditions, and survival and growth of young larvae on whorl sections of young corn plants under laboratory conditions were significantly correlated with average corn borer leaf-feeding ratings of older corn plants. This indicates that either of these methods could be used to rate plants for corn borer resistance. However, the usefulness of these methods would be limited in that plants tested are destroyed. These methods could be used successfully for testing general line performance, but other methods of rating should be employed if individual plant evaluations are necessary.

The location of young corn borer larvae was carefully observed and recorded on all plants infested in the field in 1961. Plants were divided into three areas (low, whorl, and exposed leaf) for these studies. Many workers have reported that about 80 to 100 percent of the young larvae on older plants were found in the whorl region. Data collected in the present studies indicated that this was not so on the young plants studied. Wide differences were observed in the percentages of young larvae in each area. Extent of larvae found in the whorl area ranged from 30 to 75 percent, in the low area from 16 to 63 percent, and in the exposed leaf area from 4 to 24 percent.

Bell (1954) reported that floral transition was the turning point in infestability of corn plants. However, in this study larvae were observed to survive for at least five and ten days on plants which had not reached this stage of development. Furthermore, rates of larval survival and growth were such that plant resistance levels could be determined. Stages of plant development in terms of number of visible leaves were estimated in these studies for times when plants of the ten inbred lines entered and completed floral transition. These estimations were calculated on the basis of large numbers of stem apices which were carefully removed from frozen stem samples which were collected in 1959. Examination of stained section is another method of determining when floral transition occurs in plants; however, the use of this method is not practical when large numbers of determinations are necessary. Since determinations were made in only one year, it is not known how much seasonal variation might be expected in the numbers of visible leaves when floral transition occurs. Leng (1951) reported that the number of visible leaves was a good estimate of internal plant development within but not between lines or hybrids.

Arrangements of plant leaf structures were studied for possible correlation with corn borer resistance. Since Bell (1954) reported that bulliform groups were the primary points of initial corn borer attack, the arrangements of several characteristics of these leaf structures were studied. The arrangements of bulliform hairs (area of leaf samples per bulliform hair and distance between bulliform hairs along bulliform groups), distance between bulliform groups across leaf samples, and widths of bulliform groups were examined on mature leaf blades for possible correlation with corn borer leaf-feeding ratings. The distance between bulliform groups across the leaf samples was the only characteristic which was correlated significantly with the average corn borer leaf-feeding ratings. This correlation occured in only one group of plant materials, the six single crosses. From the results obtained in these studies, it appears that none of the characteristics studied were major contributing factors for corn borer resistance. However, only one leaf position was sampled, and this was done at only one stage of plant development. Further studies on different leaves and at different stages of plant growth should be conducted. Bell (1954) reported that widths of bulliform groups appeared to be correlated with corn borer resistance on younger plants of the lines which he studied. It is possible that any of the characteristics described above might contribute to corn borer resistance to a smaller extent in some lines or to a larger extent in other lines, but these could not be detected in the present studies.

SUMMARY

Survival of larvae of the European corn borer, Ostrinia nubilalis (Hubner), was studied after five days of feeding on young corn plants which had been infested in the field during the three year period, 1959 through 1961. Three groups of plant material were included in these studies, ten inbred lines, six single crosses, and six related inbred lines. The ten inbred lines were studied in all three years, and the six single crosses and six related inbred lines were studied only during the last year. In addition to the five day survival levels on the ten inbred lines, levels of survival were also observed after ten days of feeding during the first two years of these studies. Infestations were made on several dates up until the time that the young plants had about seven to nine visible leaves.

Results of these field studies indicated that survival levels were different among the lines or hybrids in each group of plant material. These differences were significant when tested by analyses of variance. Ranked means for each group of plant material were correlated with the average corn borer leaf-feeding ratings which had been determined on older plants. These correlations were all significant.

During the last year of these studies, 1961, location of the corn borer larvae was determined on the infested plants of all three groups of plant material. Young plants were divided into three plant areas -- low (at the base of the plant or behind the leaf sheaths of those leaves with exposed ligules), whorl, and exposed leaf -- and survival was recorded in each area. Patterns of survival were observed in these plant areas within lines or hybrids, but were greatly different among the lines

or hybrids. The following average survival levels were observed in each of these three areas: low area -- 16 to 63 percent, whorl area -- 30 to 75 percent, and exposed leaf area -- 4 to 24 percent.

Stem apices were studied in 1959 for the ten inbred lines to determine the stages of plant growth at the time of floral transition. Numbers of visible leaves were estimated for the times when each line started and completed the floral transition. Different numbers of visible leaves were observed among the lines when these stages of apical development occurred. It was estimated that plants had four to seven visible leaves when they entered transition and seven to ten visible leaves when transition was completed.

The three groups of plant material which were studied in the field were also studied in the laboratory. The ten inbred lines were studied in the laboratory in 1960, and again in 1961 along with the six single crosses and six related lines. Whorl sections were removed from young plants on several dates up until plants had seven to nine visible leaves. These sections were infested in test tubes and maintained for five days at a temperature of 76° F. and a relative humidity of 78 percent. Survival levels and larval growth rates were determined on these samples. Significant differences were observed in the survival levels among the ten inbred lines in both years, and also among the six single crosses but not the six related lines in 1961. Survival levels and larval growth rates were all significantly correlated with average corn borer leaf-feeding ratings.

Corn borer survival was better on the later dates of infestation in both field and laboratory studies for all plant materials. The larval growth rates were also better on the later dates of infestation in the laboratory studies.

The arrangements of several bulliform characteristics were studied on mature leaves of all three groups of plant material for possible correlation with corn borer resistance. These characteristics included the arrangement of bulliform hairs (area of leaf per bulliform hair and distance between bulliform hairs along bulliform groups), the distance between bulliform groups across leaf samples, and the widths of bulliform groups. The distance between bulliform groups among the six single crosses was the only characteristic which was significant correlated with average corn borer leaf-feeding ratings.

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APPENDIX

Table 37. Analysis of variance for corn borer survival in the laboratory on resistant (CI31A) and susceptible (WF9) inbred lines infested with 5, 15, 25, and 35 eggs per plant[a]

Source of variation	Degrees of freedom	Mean square	F value
Replications	2	197.98	1.786
Lines	1	2336.03	21.068**
Error a	2	110.88	
Treatments	3	251.73	20.219**
Linear Regression	1	728.56	58.519**
Deviations	2	26.63	2.139
Lines x Treatments	3	34.47	2.769
Error b	12	12.45	

[a]Coefficient of variation was 9.15 percent.

*Significant at the 5 percent level of probability.

**Significant at the 1 percent level of probability.

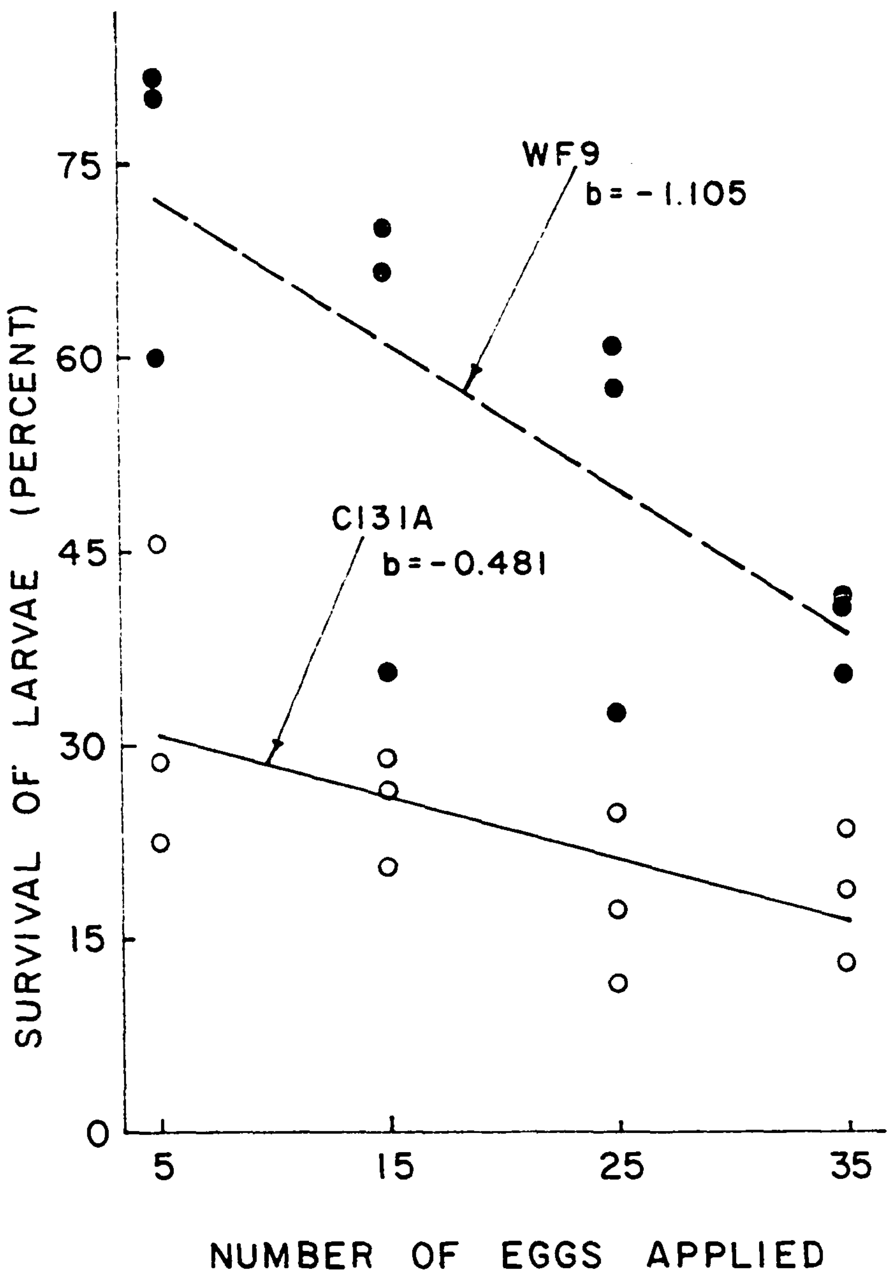

Figure 17. Average survival patterns of European corn borer larvae after five days of feeding on WF9 and CI31A plants which had been infested with different numbers of corn borer eggs in the laboratory